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Iowa State University PH.D. 1980

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The digestion of complex carbohydrates in the large intestine of the growing pig: Effects on nitrogen metabolism

by

Juan Gargallo

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GENERAL INTRODUCTION

The digestive tract consists of three functional regions: stomach, small intestine and large intestine. The low pH and pepsin initiate digestion of the protein components of the food but, except in ruminants, absorption from the stomach is minimal. In the small intestine, the food materials are broken down to simple molecules by the action of intestinal and pancreatic enzymes and final products of digestion are absorbed as they are released. Microbial activity is not important in the small intestine of the healthy animal. In complete contrast, any digestion in the hindgut is microbial (Bayley, 1978). The substrate for this fermentation is the material which has escaped absorption during its passage through the small intestine. The conditions within the hindgut - low oxygen tension and absence of readily fermentable substrates - limit the activities of the microflora to utilize the residues which have escaped enzymatic digestion in the small intestine. Under these conditions, the microorganisms release volatile fatty acids (VFA), amines and ammonia as the main fermentation products.

Classically, nutritionists have measured apparent digestibilities of feeds as indicators of potential nutritional value of feeds. The present application of more sophisticated analysis to measure the digestibilities of specific nutrient

compounds, however, demands a better understanding of the molecular changes brought about in the hindgut by the microflora. These changes may be of little nutritional consequence to the host animal.

The large intestine digesta has the largest bacterial population ($2.37 \pm 1.00 \times 10^{10}$ bacteria/g fresh content; Allison et al., 1979) and the greatest number of microbial species in the gut of nonruminant animals (Ducluzeau and Raibaud, 1975). In addition to the luminal flora, there is a mucosal flora (bacteria growing in close association with the mucosal surface and in the villous crypts) which has not been studied extensively, but it is believed to play an important role in some metabolic processes taking place in the hindgut (Drasar and Hill, 1974). Bryant (1974), working with humans and swine, concluded that the microflora of the hindgut of both species was somewhat similar to that found in the rumen. Ulyatt et al. (1975), however, reported that no protozoal population was found in the cecum and that many large bacteria were also absent.

The digestibilities of carbohydrates in the small intestine are variable, not only according to their nature (starch, cellulose, etc.) but also for each family of constituents, according to their origin (in the case of cellulose: wheat bran, wood cellulose, etc.). This variability signifies that digestive residues reaching the large intestine are highly

variable in amount and nature according to the chemical composition of dietary carbohydrates. As an example, the ileal digestibility of corn starch is much higher than the ileal digestibility of potato starch (80 vs. 65%). Thus, the energy supplied to the animal by starch digestion proceeds in variable proportion from the enzymatic digestion in the small intestine and the microbial digestion in the large intestine depending on the nature of the starch. The microorganisms primarily concerned with the breakdown of starch in the cecum and colon belong to a strain of Clostridium butyricum (Baker et al., 1950) that supplies the major source of α-amylase (Whelan and Nasr, 1951). Starch is hydrolyzed to maltose and dextrins by the action of α-amylase and, subsequently, into hexose sugars by other species of microorganisms (lactobacilli and enterococci) present in the cecum and colon. The characteristics of cellulose fermentation in the large intestine of pigs have not been studied extensively. In a review by Cranwell (1968) it was indicated that a rather old work by Trautmann and Asher, 1942, showed that the microorganism mainly responsible for cellulose fermentation in the cecum is a large, more or less spherical bacterium which is readily stained with iodine and probably belongs to the Coccaceae family. Subsequent in vitro experiments by the same authors gave more definitive knowledge of the culture requirements of this microorganism, but attempts to isolate it in pure

culture were not successful. A great deal of information is available about the cellulolytic bacteria of the rumen (Bryant, 1974), but the similarities and differences between rumen and large intestine cellulolitic flora remain to be studied. Microbial breakdown of complex carbohydrates (cellulose, starch; Hall, 1965) or more simple ones (glucose: Michel, 1961) in the digestive tract leads to the formation of organic acids. The fermentation also results in production of other compounds, such as methane and hydrogen (Levitt et al., 1974). The concentration of organic acids in the stomach is low. It remains low in the small intestine and increases abruptly in the cecum and colon (Argenzio and Southworth, 1975). VFA represent 92% of all organic acids produced in the pig large intestine (Clemens et al., 1975). In the pig, the transport of VFA through the cecal and colonic mucosa is faster than through the gastric mucosa; the absorptive process is, therefore, very efficient (Argenzio and Southworth, 1975) and complete (Farrell and Johnson, 1970). VFA certainly serves as a source of energy in the rat, because $^{14}CO_2$ is found in the expired air when ^{14}C-labeled VFA are introduced in the cecum (Yang et al., 1970). Net contribution of VFA to the animal energy needs, however, is not clear because work by Imoto and Namioka (1978) suggests that a significant fraction of VFA from the large intestine was metabolized during absorption.

There are two possible sources of N in the large

intestine, 1) dietary N that has not been absorbed in the small intestine and products of endogenous origin (digestive enzymes, desquamated cells, mucoproteins, etc.) and 2) N from blood. Generally, it has been assumed that the amino acid composition of terminal ileum digesta is rather constant because endogenous sources are predominant (Nasset, 1962). Recent studies (Holmes et al., 1974) have shown, however, that the quantity of exogenous N reaching the terminal ileum is extremely variable, depending upon the nature of ingested nitrogen. The other potential source of N in the large intestine is from blood, mainly in the form of urea. This source may play an important role in ruminal N metabolism (Ørskov et al., 1971) but its significance in the large intestine is not clear. Phenomena pertaining to N metabolism in the large intestine are quantitatively important and complex. In pigs, they lead both to a disappearance of N and most amino acids, but also to the appearance of these substances during the ceco-colic passage of digesta. In general, the disappearance of an amino acid in the large intestine is assumed to result from deamination, whereas the reappearance of an amino acid in feces corresponds to bacterial synthesis (Rerat, 1978). Microbial protein synthesis is mainly limited by the amount of fermentable energy reaching the large intestine, rather than by nitrogen which is usually present at levels more than adequate to sustain maximal

microbial growth (Mason et al., 1977). Thus, apparent nitrogen and amino acid digestibilities of a given diet are affected largely by the amount of dietary carbohydrate reaching the large intestine, as demonstrated in rats by Mendes-Pereira et al. (1977). The active microbial protein synthesis taking place in the large intestine may introduce some errors in the assessment of amino acid availability. Therefore, amino acid digestion at the terminal ileum seems to be a better method to evaluate amino acid availability than digestion at fecal level. Contrary to carbohydrate digestion, digestion of nitrogenous materials in the hindgut of nonruminants is not an efficient system from a nutritional point of view, because neither ammonia nor microbial protein can be utilized by the animal to a large extent.

Feeding high levels of nonabsorbable antibiotics does not completely eliminate intestinal bacteria, but it brings about a change in the microbial species present in the intestine and a reduction in intestinal fermentation (Kent et al., 1969). Consequently, the addition of antibiotics to the diet of nonruminants results in a decrease in starch (Mason and Just, 1976) and cellulose (Michel, 1965) digestibilities and an increase in apparent N and amino acid digestibilities (Mason et al., 1976) when compared to non-treated controls.

Dietary fiber is defined as the insoluble structural matter of plants that is resistant to animal digestive enzymes and it is generally equated to plant cell walls (Van Soest, 1975). Consequently, fiber represents a category fitting the definition and it is, therefore, very variable in both its physical and chemical properties. Plant cell walls are composed primarily of three organic fractions; cellulose, hemicelluloses and lignin. Cellulose and hemicelluloses are carbohydrates and lignin is a mixture of noncarbohydrate compounds. The old definition of "nonnutritive substances" has been abandoned because fibrous carbohydrates may be nutritively available through fermentation and they may contribute significantly to meet the energy needs of nonruminant animals. Also, it has been shown that undigestible carbohydrates may be beneficial by influencing transit of food and the environment of the lower digestive tract. The evolution of the concept of dietary fiber has been parallel to the evolution of its chemical analysis. The original concept of crude fiber was that it represented the truly undigestible part of the diet. Crude fiber analysis, unfortunately, recovers neither undigestible fractions nor all fibrous substances present in the diet. The failure of crude fiber to correlate well with the present concept of fiber is related to the extent to which the proportion between hemicellulose and lignin vary among plant cell wall types. This variation is considerable and it is largely

responsible for discrepancies between crude fiber and plant cell walls. The physical and chemical properties of plant cell wall carbohydrates have been discussed thoroughly in excellent reviews by Bayley (1978) and Van Soest (1975).

In recent years, a great deal of attention has focused on the role of fiber in the diets of humans and other non-ruminants. Values found in the literature for apparent digestibility of dietary fiber range from zero (Mitchell and Hamilton, 1933) to 97% (Poijarvi, 1944) mainly because of the different origin of the fiber studied. Also, the different analytical techniques used and the practical variability associated with most of these techniques may partially explain these discrepancies (Heller et al., 1977). An extensive review about this subject has been published recently by Fahey (1979). Cellulose represents the largest fraction of plant cell walls and it is mainly responsible for the variation in digestibility of the fiber fraction in forages and feeds. Also, cellulose can be considered as a good indicator of the fermentation potential of plant cell walls because, for a given feed, the rate of fermentation (disappearance with time) of cellulose or cell wall give practically identical rates (Smith et al., 1972). In addition to the origin of the cellulose, other factors may influence its digestibility, but to a lesser extent. According to Nehring et al. (1965), the variability between animals may play some part, because, for the

same source of cellulose, large differences in apparent digestibility are observed between littermate pigs. Live weight of pigs, beyond weaning age, does not seem to have any significant effect (Cunningham et al., 1961). Change from restricted to ad libitum feeding of pigs brings about a reduction of cellulose and energy digestibility, probably because of the modification of the rate of passage of digesta through the gut (Castle and Castle, 1956). As discussed previously, breakdown of cellulose decreases after administration of antibiotics or sulfa drugs.

The experiments reported herein were conducted to obtain a better understanding of the characteristics, limiting factors and nutritional implications of dietary cellulose digestion in the large intestine of the growing pig. The purposes for the development of a new type of cannula and the objectives of each of the four experiments are stated in the introduction within the respective sections of this dissertation.

Explanation of Dissertation Format

Section A has been published in the American Journal of Veterinary Research, 1980, No. 41 (Vol. 4), p.622. The experiment described in Section B has been submitted for publication to the Journal of Nutrition. The experiment in Section C has been published in the Journal of Animal Science No. 51 (Vol. 1),

p. 121. Two papers corresponding to the experiments described in Sections D and E have been submitted to the Journal of Animal Science. All papers are under the authorship of Juan Gargallo and Dean R. Zimmerman.

SECTION I. A SIMPLE INTESTINAL CANNULA FOR SWINE

INTRODUCTION

During the last decade, nutritionists have become increasingly interested in digestive phenomena taking place at different levels of the gastrointestinal tract. Cannulation is a widespread method used to permit sample collection for partial digestibility studies and to make flow measurements in the intestinal tract. Either T-piece cannulae, with markers for spot sample collection, or reentrant cannulae for total sample collection are used. Representative samples can be obtained from reentrant cannulae because all digesta passes through the cannulae, whereas in T-piece cannulae, physical separation of digesta components may occur when flow is diverted. Reentrant cannulae, however, have certain disadvantages. Relatively complex surgical procedure is involved and about 25% of the preparations in pigs are not suitable for sample collection (Low, 1977). It also is difficult to maintain an acceptable food intake for a long period after the operation (Laplace and Borgida, 1976). An additional problem arises in pigs given high-fiber diets because occlusion of the cannula and consequent suppression of the appetite often occur. Therefore, if high-fiber diets are fed to pigs for extended periods, T-piece cannulae are the best choice for digestibility studies.

Single T-piece cannulae have been used for a long time

for ruminal fistulation (Quin et al., 1938; Stoddart et al., 1951; Binns and Lynn, 1959). Also, intestinal cannulation has been reported (Hinkson, 1970; Jones et al., 1971; Furuya et al., 1974; Decuypere et al., 1977; Livingstone et al., 1977). This report describes a cannula for the pig that overcomes some of the problems experienced with other types of cannulae.

MATERIALS AND METHODS

The cannula is made of rigid polyvinylchloride (PVC) fittings commonly used in plumbing. These parts are light, easy to obtain, and inexpensive. The cannulae are easy to make, and are well tolerated by the animals.

The parts of a cannula, in order of assembly from bottom to top, are: base, stem, external washer, thread adaptor, and cap (Figure 1). The base and adaptor are PVC fittings for 15.9 mm outer diameter by 12.7 mm inner diameter PVC tubing. The external washer is made from a 3.2 mm extruded acrylic sheet, and the cap is from a polyethylene bottle.

The base is made by cutting off one-half of the longitudinal channel of a 3-way connection, and rounding and thinning the cut surfaces. This results in a base with two gutter-type flanges (total length of 45 mm). The stem is a 35 mm length of PVC tubing, 15.9 mm outer diameter and 12.7 mm inner diameter, which is slip-fit to the base. The stem and base form the part of the cannula that is implanted by surgical procedure. The connections are joined with PVC cement that forms a strong bond in a few minutes.

The external washer is a circular piece of extruded acrylic sheet with a diameter of 55 mm and a thickness of 3.2 mm. A hole of 19 mm diameter is drilled in the center. The washer fits tightly over the lower rim of the threaded adaptor.

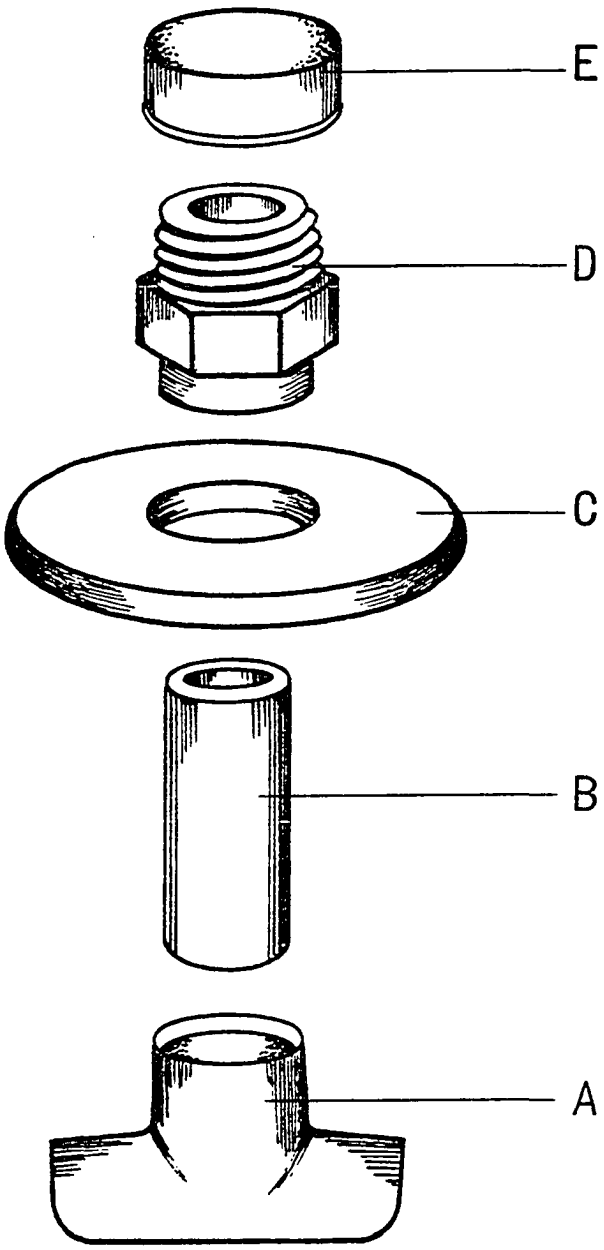

Figure 1. Parts of a cannula in order of their assembly: A - Base, B - Stem, C - External washer, D - Thread adaptor and E - cap

The adaptor is a PVC line terminal from which 5 mm of the threaded end has been removed to decrease the external projection of the cannula from the body wall. The adaptor is permanently fixed to the stem with PVC cement during the operation.

Surgical procedure: Ten crossbred gilts weighing 30 to 35 kg were fasted for 24 hr before the operation. Halothane was given to the pigs to induce and maintain surgical anesthesia. With the pigs in left lateral recumbency, the right paralumbar fossa was shaved and disinfected. A 7 cm incision was made starting about 4 cm below the transverse process of the 5th lumbar vertebra and proceeding in a ventral direction. The abdominal muscles were incised parallel to the direction of their fibers. The terminal part of the ileum was exteriorized using the cecum as anatomical reference to locate it. A 2 cm incision on the antimesenteric side of the ileum was made approximately 10 cm cranial to the ileocecal valve. The cannula was inserted into the ileum and a double purse string suture (2/0 surgical gut) was placed around the stem. The exteriorization was made half way down the incision and 3 cm cranial, using the technique described by Markowitz et al. (1959). When exteriorizing the cannula, special care was taken so that the flanges of the base brought the ileum in close contact with the peritoneum to obtain good adhesion of the serosal layers at this point.

The abdominal incision was closed using size 0 cotton thread in a continuous lockstitch, and the skin, using the same material in an interrupted suture. The adaptor, already fitted with the external washer, was then glued to the exteriorized stem. Antibiotics were injected intramuscularly on 3 consecutive days.

A normal level of feed intake was attained 3 to 5 days after the surgical procedure and pigs were considered suitable for sampling 7 days later.

RESULTS AND DISCUSSION

Cannulae described in the literature differ markedly in characteristics and shape, but usually are made with molds or by hand modeling of the materials, involving a considerable amount of labor. On the other hand, and because of the particular idiosyncrasy of swine, cannulae are likely to be dislodged unless they are well-anchored to the body wall (Moir and Doyle, 1978).

Cannulae made of soft materials were well-tolerated by the pig, and little leakage was evident, but they were dislodged by the animal, even when secured internally. Acrylic plastic was too fragile. It allowed considerable leakage and was difficult to secure to the body wall.

After attempts with several types of cannulae, the one described in the present study closely approached the ideal characteristics of simplicity, light weight, rigidity, toughness, good tolerance by pigs and minimal leakage.

Pigs fitted with PVC cannulae were kept in metabolism stalls for 40 days (Figure 2). They were used for large-intestine digestibility trials with frequent infusion and sampling of materials through the cannulae. When the trials were completed, the pigs were transferred to smooth-walled pens and raised to market weight. During the entire period, the pigs showed no digestive disturbances. Cannulae remained

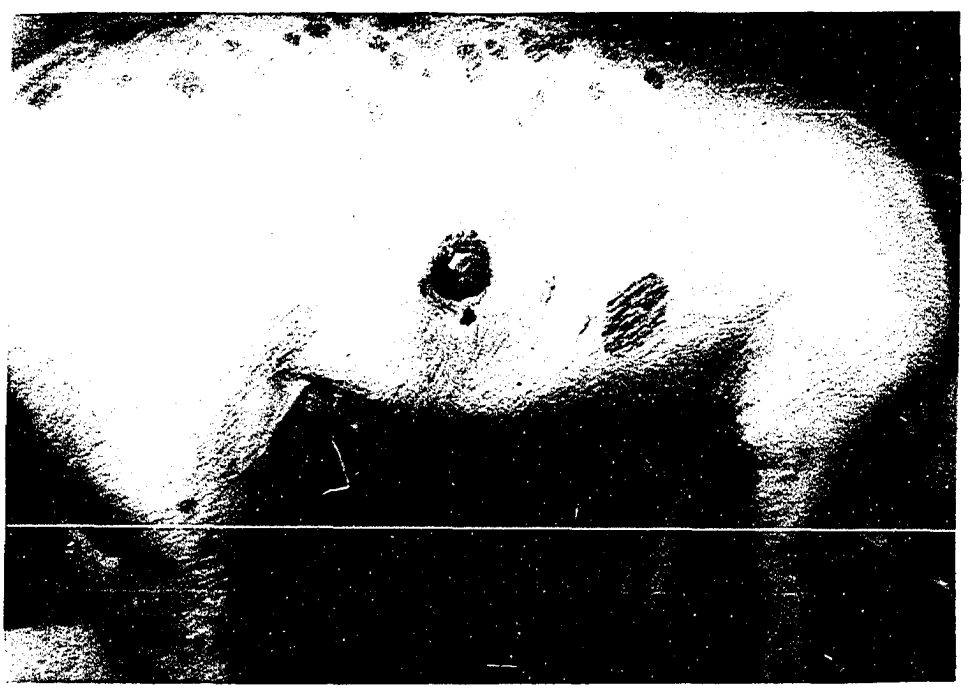

Figure 2. Cannulated pig in a metabolism stall. View of the right side 42 days after surgery

well-anchored to the body wall, and the amount of leakage was minimal. Factors that minimized leakage were the small diameter of the fistula, minimal movement of the cannula, light weight, and projection of only 2.5 cm from the body wall.

The pigs showed no macroscopic lesions at any site of the gastro-intestinal tract when euthanatized other than localized enteritis around the cannulation site. Occasionally, adhesions of an intestinal loop to the parietal peritoneum were found around the incision area.

SECTION II. EFFECT OF CASEIN AND STARCH INFUSION IN THE LARGE INTESTINE ON NITROGEN METABOLISM OF GROWING SWINE

INTRODUCTION

The presence of a microbial population in the lower intestine and subsequent voiding of microbial cells in the feces has been known for a long time (McNeal et al., 1909). Its nutritional significance, however, has not been studied until recently. The microbial population in the rumen and its function have been studied extensively because of the prominent role it plays in nutrient utilization by ruminant species. Knowledge of ruminal metabolism has stimulated investigations of the fermentation taking place in the lower tract of ruminants. Several reports have shown that cecal fermentation in sheep is similar to that in the rumen (Ørskov et al., 1970; Thornton et al., 1970; Hecker, 1971). The microflora in the hindgut of sheep have more than adequate amounts of nitrogen (N) in relation to energy (Mason et al., 1977). Therefore, in sheep, the presence of fermentable energy in the cecum, supplied either by the diet (Thornton et al., 1970) or by infusion via a cannula (Ørskov et al., 1970; Rerat, 1978), results in an increase in fecal N, mainly in the form of bacterial protein.

The quantity of exogenous N reaching the ileum in the pig is extremely variable. It varies with the nature of the N ingested, ranging from 10 to 40% of N intake (Zebrowska, 1973). Starch constitutes the major substance in practical pig diets.

Its digestibility, measured at the terminal ileum of the pig, is about 90 percent (Holmes et al., 1974; Keys and DeBarthe, 1974), considerably higher than the digestibility observed with ruminants fed the same type of diets (Ørskov et al., 1970). Consequently, the fermentation process taking place in the hindgut of nonruminants is somewhat different from that taking place in ruminants.

In swine, the role of the large intestine and of its microflora in nutrient utilization have been long debated because of the lack of conclusive data in both direct (ileal cannulation) and indirect (antibiotic suppression of intestinal flora) studies (Rerat, 1978). The addition of potato starch to the diet of growing pigs results in an increase in total N and α-amino N excreted in the feces (Mason et al., 1976), suggesting a more active bacterial protein synthesis as is the situation in ruminants. However, no estimates have been made of the amount of microbial protein synthesized per unit of starch fermented. Other reports have suggested that, actually, ileal and fecal N digestibilities are similar and that the differences reported are mainly related to technical problems relative to the location of the ileal cannula (Braude et al., 1975; Poppe and Meier, 1977).

The purpose of our experiment was 1) to investigate the extent and effect of corn starch and casein fermentation on N

metabolism in the large intestine of the pig, and 2) to quantify the influence of starch fermentation on N excretion.

MATERIALS AND METHODS

Eight crossbred, female pigs with an average body weight of 40 kg were housed in metabolism cages in an environmentally controlled room. They were fitted with ileal cannulae as described elsewhere (Gargallo and Zimmerman, 1980a), and allowed to recover for 2 weeks before the experiment was started. Size 12 Foley catheters[1] were placed in the bladder throughout the experiment for total urine collection.

All pigs were fed daily the basal diet (Table 1) at a level of 4% of their body weight in two equal feedings at 12-hr intervals. Treatments were infusions via the cannula into the terminal ileum of 1) saline, 2) 20 g of lactic casein, 3) 50 g of corn starch, and 4) 20 g of lactic casein[2] plus 50 g of corn starch. These substances were suspended in 150 ml of saline, warmed to 37 C and infused by gravity. Pigs were infused every 8 hours for 7 days. Infusions lasted approximately 10 minutes.

During the last 2 days, total collections of feces and urine were made. At the end of the 7-day period, pigs were weighed, bled from the anterior vena cava 4 hr postprandially, and switched abruptly to another treatment. At the end of the experiment, pigs were maintained under the same feeding regime for a 3-day period, at the end of which a 12-hour collection of

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[1]C. R. Bard Inc., Murray Hill, N.J.

[2]Milk Specialties, Inc., Box 278, Dundee, Il. 60118.

Table 1. Basal diet composition

Item	International Reference No.	Percent
Ingredients		
Ground yellow corn	4-02-935	78.20
Soybean meal, dehulled	5-04-612	18.50
Calcium carbonate	6-01-069	.90
Dicalcium phosphate	6-01-080	1.25
Iodized salt	6-14-013	.50
Vitamins and minerals[a]	-	.55
Chromic oxide	-	.10
TOTAL		100.00
Calculated analysis		
Crude protein, %		16.24
Calcium, %		.72
Phosphorus, %		.54
Metabolizable energy, kcal/kg		3085

[a]Contribution per kilogram of diet: vitamin A, 2204 IU; vitamin D_2, 550 IU; riboflavin, 3.3 mg; Ca pantotenate, 8.8 mg; niacin, 16.5 mg; vitamin B_{12}, 11 µg; choline chloride, 397 mg; zinc, 100 ppm; iron, 50 ppm; manganese, 27.5 ppm; copper, 5 ppm; iodine, .75 ppm.

ileal contents was made.

Plasma urea N was measured by the methods described by Marsh et al. (1965). Feces and ileal contents were collected in 1N HCl, homogenized, and a 10% aliquot freeze-dried. Dry matter and N were determined by the A.O.A.C. procedures (1975). Chromium was determined by atomic absorption spectrophotometry,[1] after wet ashing of samples. RNA was measured by the method

[1]Perkin-Elmer, Model 460.

described by Fleck and Munro (1962) and total protein was determined by the method described by Gehrke and Wall (1970). This method estimates the total amino acid content of the 6N HCl hydrolysate. Fecal and ileal starch was gelatinized by autoclaving an aqueous suspension of the sample for 30 minutes. Hydrolysis was done by incubating at 50 C for 48 hours with amyloglucosidase (EC 3.2.1.3) buffer solution[1] (pH 4.54). Glucose was measured by the glucose oxidase (EC 1.1.3.4) method .[2] Urine was collected into brown glass bottles containing 25 ml of concentrated HCl and 25 ml of toluene. A 10% aliquot was retained and stored at -20 C until analyzed. Urea and ammonia N were determined simultaneously by an automated method (Burnette et al., 1976). Orotic acid was measured by a colorimetric method described by Stajner et al. (1968).

The experimental data were treated statistically by analysis of variance as two 4 x 4 latin squares. Treatment effect was divided into casein and starch infusion main effects and their interaction. Significance reported refers to main effects and interaction, not to differences between

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[1]Composition of the buffer solution (per 1000 ml): 8 g amyloglucosidase (Sigma Co., St. Louis, MO); 11.7 ml acetic acid; 8.73 g sodium acetate; .08 g Thymol; 1.3 g sodium azide; .1212 g sodium penicillin (Gibco, Grand Island, NY); .2703 g streptomycin (Gibco, Grand Island, NY); .01 g amphotericin B (Sigma Co., St. Louis, MO).

[2]Sigma Chemical Company, St. Louis, MO. Technical Bulletin No. 510.

individual treatments. Occasionally, single degree of freedom comparisons were used to contrast treatment means.

RESULTS AND DISCUSSION

Apparent small intestine, large intestine, and total digestibilities of the chemical components of the basal diet were calculated by using chromium oxide as nonabsorbable marker (Table 2). Average fecal recovery of chromium was 96%, although it was somewhat variable (coefficient of variation, 20%). A net disappearance in the hindgut was found for all chemical fractions studied, suggesting that, in swine, the large intestine plays an important role in the process of nutrient digestion. Apparent dry matter digestibilities in the small and large intestine were very similar to those found with semi-purified diets containing corn starch and corn sugar when fed to pigs fitted with reentrant cannulae (Holmes et al., 1974). In sheep, also fitted with reentrant cannulae, dry matter digestibility in the small intestine of a diet much higher in fiber (oat hulls-alfalfa) was considerably higher

Table 2. Apparent digestibilities of chemical components of basal diet (%)[a]

Item	Small intestine	Large intestine	TOTAL
Dry matter	68.8 ± 8.9	48.1 ± 18.5	85.2 ± 1.5
N	73.9 ± 13.0	28.7 ± 25.6	83.0 ± 2.6
Total protein	79.8 ± 5.4	19.5 ± 29.3	85.1 ± 2.2
Corn starch	90.5 ± 4.4	85.3 ± 10.1	98.5 ± .8
RNA	17.3 ± 28.1	28.6 ± 27.3	46.0 ± 7.1

[a]Values shown are the mean ± SD, n = 8.

than that exhibited by pigs in our experiment (85% vs. 69%) (Thornton et al., 1970). In the same report, dry matter digestibility in the large intestine of sheep was lower than we obtained with pigs (15% vs. 48%). The large differences in the digestive tract between these two species may account for these discrepancies. Apparent N digestibility was lower in the small intestine and higher in the large intestine than reported for semipurified diets, in which all protein came from soybean meal (Holmes et al., 1974). This effect is probably because of the lower digestibility of zein compared with soybean meal protein. Apparent digestibility of total protein (amino acids) in the small intestine was higher than apparent N digestibility, possibly as a result of the transfer of endogenous nitrogen-containing compounds (mainly urea) from blood into the lumen (Ewe and Summerskill, 1965), although this aspect has not been investigated in swine. Apparent total protein digestibility in the hindgut was lower than N digestibility because of the active microbial protein synthesis taking place in these reservoirs. It is generally accepted that corn starch is totally digested by pigs, but there are some discrepancies about the amount that is digested in the large intestine. Our data indicate that about 10% of dietary corn starch reaches the hindgut and disappears there, which agrees closely with other literature values (Keys and DeBarthe, 1974). Other reports however, indicate that less than

2% of dietary starch reaches the hindgut (Holmes et al., 1974; Sambrook, 1979). Further work is needed in this area to clarify the discrepancy. The apparent digestibility of the RNA present in the basal diet was considerably lower than reported in calves or sheep infused abomasally with RNA (Bergen, 1978). This difference is explained partly by the low RNA content of the basal diet (7.11 g/kg) and partly because its availability was lower than it would be for purified RNA.

Table 3 shows the results of the 2-day N balance for each treatment. Nitrogen infused via the cannula as casein was considered as intake for balance purposes. The infusion of casein increased ($P<.05$) the N retained by the experimental animals. Recent studies conducted with germ-free and conventional piglets (Deguchi et al., 1978a, 1978b), showed that ammonia N formed in the large intestine as a result of microbial activity can be utilized for the synthesis of all essential and nonessential amino acids, except threonine. In our experiment a large fraction of the N of infused casein disappeared from the large intestine, probably being deaminated by the intestinal flora to yield ammonia and various amines (Fauconneau and Michel, 1970).

With our experimental conditions, it seems unlikely that the de novo amino acid synthesis from ammonia could account for a large fraction of the increase in N retention of pigs

Table 3. Effect of cecal infusion of corn starch and casein on N metabolism[a]

Item	Treatment				
	Blank	Starch	Casein	Starch +casein	SE
Total N					
Intake, g	103.2	106.8	122.2	120.9	
Retention, g[b]	53.9	58.2	64.9	67.1	2.8
Excretion, g[b]	49.2	48.6	57.3	53.8	2.9
Fecal, g[c]	15.7	17.1	16.5	19.0	.9
% of excretion[c]	32.6	37.4	28.6	35.9	2.7
Urinary, g[d]	33.5	31.4	40.7	34.7	2.9
% of excretion[c]	67.3	62.5	71.3	64.0	2.7
Urea, g[e,f]	26.9	24.7	34.6	29.1	2.2
Ammonia, g	1.9	1.8	2.6	2.2	.3
Unaccounted, g	4.9	4.6	3.5	4.3	.7

[a]Values shown are totals of a 2-day collection period.

[b]Casein effect, $P<.05$.

[c]Starch effect, $P<.05$.

[d]Casein effect, $P<.10$.

[e]Starch effect, $P<.10$.

[f]Comparison casein vs. rest, $P<.05$.

infused with casein (Kornegay et al., 1970; Wehrbein et al., 1970). In addition, no parallel increase in average daily gain was observed in these pigs, although differences may have been obscured by the large variability associated with this measurement (coefficient of variation, 27%). It is also possible that occasional wastage occurring during the infusion process could result in overestimation of N retained. No conclusive explanation could be given for the increased N retention observed when casein was infused.

Fecal N, expressed both in absolute amounts and in percentage of total N excretion, increased ($P<.05$) when corn starch was infused. The infusion of casein did not affect fecal N ($P>.10$), indicating that it was completely digested in the large intestine. No interactions were found between casein and corn starch infusion probably because N was not a limiting factor in the process of starch digestion. It is known that in ruminants fed high energy diets, N may be a limiting factor for microbial growth in the rumen, even though N is supplied to the rumen in the form of urea via saliva and blood (Ørskov et al., 1971). In treatment 1 (saline infusion) approximately 8 g of N disappeared from the large intestine in a 2-day period. This amount is much larger than the increase in fecal N observed when corn starch was infused. It seems, then, that in practical conditions, N would

never limit microbial growth in the large intestine of pigs.

Table 4 shows the fecal total protein (amino acids) data for each treatment. A significant starch infusion effect ($P<.05$) was found. Casein did not affect fecal total protein, supporting the idea that infused casein was totally digested and absorbed in the large intestine. Fecal total protein (16% N content) represented 71.5% $\pm$ 3.7 of total nitrogen. Also, differences in fecal N between treatments can be explained for by differences in fecal total protein.

Several techniques have been proposed to estimate the microbial fraction of digesta and feces (Smith, 1975). Variation in diaminopimelic acid (DAPA):total N ratios between one pure strain of rumen bacteria and another (Synge, 1953) is much larger than the variations in nucleic acid N:total N ratios (Smith, 1969). Also, in protozoa-free calves the ratio RNA N:total N was considerably less variable than DNA N:total N or nucleic acid N:total N (McAllan and Smith, 1972). Because of these relationships and the almost complete absence of protozoa in the large intestine of pigs (Ulyatt et al., 1975) RNA was chosen as an indicator of microbial protein in this experiment. Corn starch infusion increased ($P<.10$) fecal RNA (Table 4), but a large variability was observed between individuals (coefficient of variation, 30%). The ratio RNA N:total protein N in feces was .128 $\pm$ .013 which is very similar to the .108 $\pm$ .012 found for the microbial

Table 4. Effect of cecal infusion of corn starch and casein on fecal total protein and RNA, g/2 days

Treatment	Fecal total protein[a]	Fecal RNA[b]
Blank	67.0	7.8
Starch	82.1	9.3
Casein	71.2	8.2
Starch + casein	87.1	9.1
SE	7.7	.8

[a]Starch effect, $P<.05$.

[b]Starch effect, $P<.10$.

population present in the rumen of protozoa-free calves (McAllan and Smith, 1972). Therefore, it seems that most of the total protein found in feces of experimental pigs was accounted for by protein of microbial origin. Because of a high correlation ($r = .95$, $P<.001$) observed between fecal RNA and fecal total protein, fecal RNA was a very good indicator of microbial protein present in feces of pigs in this experiment. However, this may not be the case when feeding high levels of a poorly digested protein source because large amounts of residual feed protein would be present in feces.

Fecal starch was not affected by the experimental treatments (overall mean $\pm$ SE, 15.9 $\pm$ 1.0 g/2 days), indicating

that the infused corn starch was totally digested. The capacity of the hindgut of sheep to digest large amounts of infused carbohydrates has been described several times (Ørskov et al., 1970; Thornton et al., 1970), but there are no reports dealing specifically with starch digestion in the large intestine of swine. The maximum capacity to digest corn starch in a 50 kg sheep is 138 g daily (Ørskov et al., 1970), which compares favorably with 150 g daily observed for pigs in our experiment, even though maximum digestion capacity was not determined. From differences in total fecal protein between corn starch-infused and noninfused pigs, we calculated that digestion of 100 g of corn starch in the large intestine increases fecal total protein (microbial protein) by 5.2 grams. This value is similar to the 5.5 g of bacterial protein synthesis per 100 g of corn starch fermented in the large intestine of sheep, as reported by Ørskov et al. (1970), assuming an average N content for bacterial protein of 18% (Purser and Buechler, 1966). In the rumen, the increase in microbial protein when 100 g of carbohydrate are digested ranges from 5 to 9 g (Hungate, 1966).

The infusion of casein increased ($P<.10$) urinary N (Table 3), whereas starch infusion showed a trend towards decreasing urinary N, especially when administered with casein, but no significant casein x starch interaction was found. Expressing

the same data as a percentage of N excretion, a significant decrease ($P<.05$) was observed for this parameter when corn starch was infused. Urinary urea N represented 81.9% $\pm$ 2.9% of urinary N and showed a decrease in total excretion ($P<.10$) when corn starch was infused. Differences in urinary N between treatment can be accounted for by differences in urinary urea N. Urinary ammonia N and urinary unaccounted N were not affected by treatments to any appreciable extent ($P>.10$). These results indicate that urinary urea was the route of excretion of the infused casein N that was neither retained nor voided in the feces as microbial protein.

The urea cycle is the major pathway for ammonia detoxication in terrestrial mammals and the main mechanism for urea synthesis. Because normal animals use only a part of their urea cycle capacity, they can make rapid adjustments to varying needs for urea synthesis (Visek, 1979). In rats with adequate levels of amino acids in their diets (especially arginine), urinary orotic acid is an indicator of the amount of ammonia being detoxified by the liver via the urea cycle (Visek, 1979). It has been proposed (Visek, 1979) that the decrease in orotic aciduria observed in rats fed starch-based diets is the result of an increase in the amount of intestinal ammonia being converted to microbial protein and, consequently, less need for ammonia detoxification by the liver. Treatment means for urinary orotic acid are shown in Table 5. No

Table 5. Effect of cecal infusion of corn starch and casein on plasma urea N and urinary orotic acid

Treatment	Plasma urea N,[a,b] (mg/dl)	Urinary orotic acid,[c] (mg/2 days)
Blank	13.5	18.0
Starch	13.1	17.2
Casein	13.3	22.0
Starch + casein	14.6	17.5
SE	.4	1.7

[a]Comparison starch + casein vs. rest, P<.05.

[b]Interaction starch x casein, P<.05.

[c]Comparison casein vs. rest, P<.05.

statistical significance was found for casein and starch main effects or interaction. However, treatment 3 (casein infusion) resulted in a higher (P<.05) orotic aciduria when compared with the other treatments. A high correlation (r = .82, P<.01) was found between urinary urea N and urinary orotic acid. Therefore, these results indicate that an increase in the activity of the urea cycle was responsible for the increase in urinary urea excretion observed when casein was infused.

Plasma urea N did not parallel the pattern described for urinary urea N (Table 5). The infusion of corn starch plus

casein resulted in an increased plasma urea N concentration when compared with the rest of the treatments (interaction corn starch x casein, $P<.05$), but no casein infusion effect was observed. This discrepancy was unexpected and, certainly, more information is needed about the correlation between urea cycle activity and plasma urea concentration to explain this response.

In summary, the large intestine of pigs can digest amounts of protein and carbohydrate larger than usually present at that level of the digestive tract. The extent of the fermentation taking place in these reservoirs affects N metabolism by modifying the amounts of N excreted as fecal bacterial protein and urinary urea.

SECTION III. EFFECTS OF DIETARY CELLULOSE AND NEOMYCIN ON FUNCTION OF THE CECUM OF PIGS

INTRODUCTION

Until recently, dietary fiber was considered of little or no nutritional value for many simple stomached animals, including man and the pig. Early reports (Woodman and Evans, 1947; Forbes and Hamilton, 1952), however, showed an apparent digestibility of the plant cell walls by pigs as high as that reported for ruminants. Later, enough evidence was obtained to prove that dietary fiber had nutritional value and that it contributed to the maintenance energy requirement of monogastric herbivores and man (Johnson and McBee, 1969; Faichney, 1969; Farrell and Johnson, 1970; Yang et al., 1970; Imoto and Namioka, 1978). In pigs, dietary fiber is digested mainly in the large intestine by fermentation, and the volatile fatty acids (VFA) produced are absorbed from the cecum and colon (Cranwell, 1968; Argenzio and Southworth, 1975). The great variability in chemical composition of different fiber sources and the strong interactions between their constituents makes their study difficult. Therefore, to assess the nutritional role of natural fiber sources, more knowledge is needed about their individual fractions.

The objective of the present study was to evaluate the effect of the dietary level of cellulose, the major component of plant cell wall, upon 1) plasma urea nitrogen (N), 2) apparent digestibilities of dry matter and cellulose, and

3) cecal concentration of free ammonia N and VFA.

Also, the effect of neomycin on the parameters mentioned was studied to estimate the extent and significance of the type of fermentation taking place.

MATERIALS AND METHODS

Six crossbred, castrated male pigs with an average body weight of 40 kg were housed in smooth-walled pens in an environmentally controlled room. They were fitted with cecal cannulae made of acrylic plastic (1.9 cm inner diameter) and allowed to recover for 10 days before the experiment was started.

All pigs were fed daily the basal diet at a level of 3% of their body weight (Table 1). The basal diet contained .1% chromic oxide. The dietary treatments were cellulose (Solka-floc)[1] additions at levels of 2, 10 and 18% of the weight of the diet. Animals were assigned randomly to the dietary treatments and fed at 12-hr intervals. During the last 18 days of the experiment, 150 mg/kg of body weight of neomycin sulfate was administered daily, 100 mg in the feed and 50 mg directly into the cecum via the cannula.

The experiment lasted 48 days; samples were collected every 4th day. Pigs were bled from the anterior vena cava. Plasma was obtained and stored at -20 C until analyzed for urea N by the method of Marsh et al. (1965). Fecal samples were collected in glass jars containing 1N HCl and stored at

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[1]Brown Co., Des Plaines, IL. Chemical composition (%): NDF, 92.5; ADF, 82.1; ADL, 3.0; cellulose, 78.9; hemicellulose, 10.4.

-20 C until analyzed for dry matter and cellulose by the detergent fiber method (Van Soest, 1963; Van Soest and Wine, 1968). Cecal contents were sampled every 3 hr in the 12-hr interval between the morning and evening feedings. Fifty milliliters of cecal fluid were strained immediately after being collected, fermentation was stopped with one drop of 12N H_2SO_4 per 5 ml of fluid, and samples were stored in plastic vials at -20 C until analyzed for ammonia N and VFA. Ammonia N was analyzed by the method described by Clare and Stevenson (1964). VFA were measured by gas chromatography using a Perkin-Elmer 900 equipped with a column packed with SP-1200/H_3PO_4 on Chromosorb W AW[1]. Amyl alcohol was used as internal standard.

The data were analyzed as a split-plot design. The cellulose levels were main-plot treatments, and the repeated measurements were subplot treatments. Test of significance for the subplot elements were made by using conservative degrees of freedom as described by Geisser and Greenhouse (1958).

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[1]Supelco, Inc., Bellefonte, PA.

RESULTS AND DISCUSSION

Neither dietary cellulose nor the administration of antibiotic affected plasma urea N (PUN) values (Table 6). The effect of dietary protein level on PUN has been well documented (Bodwell, 1975), but the effect of dietary fiber is not clear. The amount of urea reaching the cecum via the ileum is very small (Gibson et al., 1973), but there is urea secretion into the large bowel with breakdown to ammonia and bicarbonate. This ammonia can be utilized by bacteria or reabsorbed by a nonionic diffusion process (Brown et al., 1971; Castell and Moore, 1971) and reconverted to urea in the liver. Results of this experiment

Table 6. Effect of dietary cellulose level on plasma urea N and cecal ammonia N, mg/dl

Cellulose level, %	Plasma urea N[a]		Cecal ammonia N[b]	
	No antibiotic	antibiotic[c,d]	No antibiotic	antibiotic[d,e,f]
2	13.8	13.5	11.1	16.9
10	13.7	14.4	9.3	19.6
18	14.0	14.0	9.7	15.3

[a]Standard error of the difference between two treatment means = ± 2.6.

[b]Standard error of the difference between two treatment means = ± 3.4.

[c]Standard error of the antibiotic effect = ± 1.1.

[d]Neomycin sulfate, 150 mg/kg body weight daily.

[e]Standard error of the antibiotic effect = ± 2.2.

[f]Antibiotic effect, $P<.01$.

suggest that variations in the cellulose content of the diet do not alter the PUN concentration in pigs.

Cecal ammonia N (Table 6) was a variable parameter. Differences among treatments were present, but none of these differences approached significance ($P>.10$). Fiber and less digestible carbohydrates pass through the small intestine into the cecum and colon where bacteria ferment them to obtain energy. Ammonia supplies N to the bacteria. Fiber causes ammonia N to be retained in the lumen of the bowel either by facilitating its dilution or by its incorporation into protein (Visek, 1978). Nolan et al. (1976), using labeled ammonia in sheep, found that the N for microbial growth in the cecum is partly derived from blood urea N, but the main source is from the deamination of digesta. Data in Table 6. along with the previous points suggest that cecal free ammonia N increased as fermentation is slowed by neomycin, but the ammonia N increase does not measurably affect the urea pool in the body as indicated by plasma urea N concentrations (Kornberg et al., 1952). The cecal ammonia N values obtained agree closely with those presented in the literature for animals under similar experimental conditions (Farrell, 1973). It is noteworthy that our data were obtained with pigs severely restricted in protein and energy intake. The values for cecal ammonia N concentration applicable to

pigs fed a high-protein, high-energy diet ad libitum remain to be determined.

The cecal ammonia N pattern between two meals was very consistent throughout the experiment and similar for the three diets (Figure 3). After an initial slight decrease 3 hr postprandially, the concentration of ammonia N in the cecum rose significantly ($P<.01$) peaking at 6 hr, probably because extensive deamination of digesta from the meal was taking place during that period. After 6 hr, the concentration declined steadily until reaching the original level. At 12 hr, the value was slightly lower (not significantly) than at feeding time, probably because of an effect of sampling.

When neomycin was administered, cecal ammonia N increased sharply ($P<.01$). Although neomycin has been reported to reduce fecal urease activity (Evans et al., 1966), a net increase in cecal ammonia N occurred. The main contributing factor to this effect is probably a decrease in bacteria-fixed N as a result of decreased bacteria number and activity. There was no buildup of urea in the cecal content, which suggests that ureolysis was taking place independently of the presence or absence of antibiotics.

The coefficients of apparent digestibilities for dry matter and cellulose are shown in Table 7. Both parameters

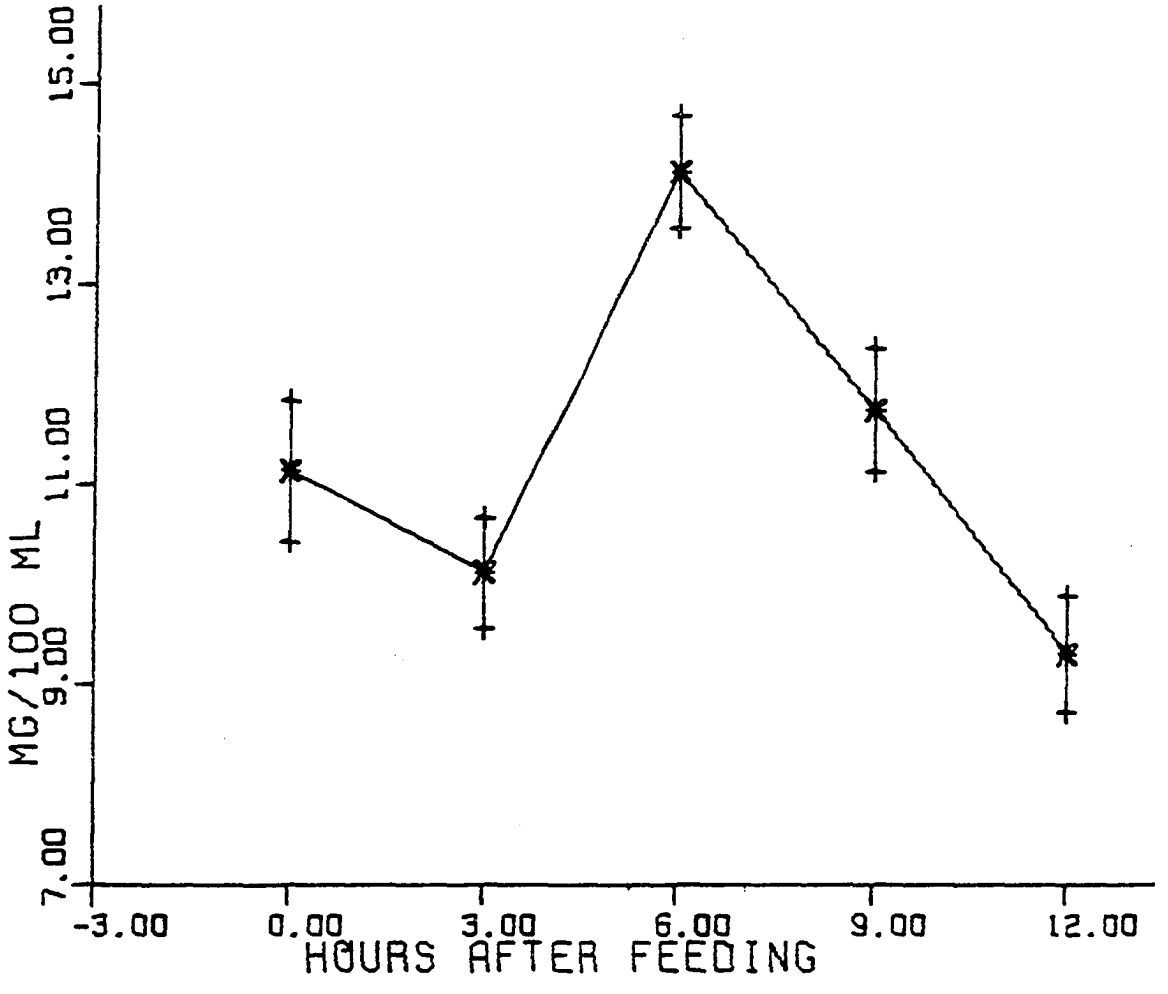

Figure 3. Cecal ammonia N pattern between feedings. Every point is the average of three dietary treatments. The range for every point represents the ± standard error of the mean obtained from 72 observations

Table 7. Effect of dietary cellulose level on apparent dry matter and cellulose digestibility, %

Cellulose level, %	Dry matter[a,b]		Cellulose[b,c]	
	No antibiotic	antibiotic[d]	No antibiotic	antibiotic[e,f]
2	83.9	82.0	42.4	.0
10	75.9	73.5	21.7	.6
18	68.2	70.7	10.4	2.8

[a]Standard error of the difference between two treatment means = ± 1.1.

[b]Linear and quadratic effect of cellulose level, $P<.01$.

[c]Standard error of the difference between two treatment means = ± 4.0.

[d]Standard error of the antibiotic effect = ± 2.2.

[e]Standard error of the antibiotic effect = ± 11.2.

[f]Antibiotic effect, $P<.01$.

decreased significantly (linear and quadratic effect, $P<.01$) as dietary cellulose increased. The addition of neomycin completely arrested the digestion of cellulose, which corroborates the microbial origin of fiber digestion, as previously found *in vivo* (Friend *et al.*, 1963) and *in vitro* (Michel, 1965). However, the experiment was not sensitive enough to show significance for the consequent changes in dry matter digestibility. In spite of the alteration in the intestinal

flora created by the antibiotic, none of the pigs showed gross digestive disturbances.

Dry matter digestibiltiy coefficients were similar to those reported in the literature (Farrell and Johnson, 1970; Farrell, 1973), but, concerning cellulose digestibility, there are some discrepancies. Farrell and Johnson (1970) reported similar digestibility coefficients for cellulose when either 8 or 26% of cellulose as Solka-floc was present in the diet. Farrell (1973) found identical cellulose digestibility coefficients for diets containing from 0 to 100% of ground lucerne. More recently, however, Schneider and Kirchgessner (1977) studied the relationship between the concentration of all plant cell wall constituents and dry matter digestibility of 36 swine feeds and found a linear relationship on a logarithmic basis. Therefore, cellulose digestibility was related to dietary cellulose in an exponential fashion.

In our study, the total amount of cellulose digested daily averaged 18, 35 and 32 g/pig for treatments 1, 2 and 3, respectively, suggesting, in concordance with the findings of Schneider and Kirchgessner (1977), that dietary cellulose level and its digestibility are inversely related. Also, it seems that, beyond a certain level at which maximal gut distension is attained and, consequently, the rate of passage is increased, cellulose digestion capability reaches a plateau.

Differences in cecal VFA concentrations (Table 8) among pigs fed different fiber levels were not significant ($P>.10$). Isobutyrate and isovalerate were present in unmeasurable amounts. The values obtained agree closely with literature values in cases in which the same type of diets were fed (Etienne, 1969; Farrell, 1973). These data show a trend that indicates that cecal acetate decreased as cellulose digestion increased, and that the intermediate level of dietary cellulose (10%) gave the greatest cecal concentrations for the rest of the VFA measured. The effect of dietary cellulose levels upon VFA concentrations has not been clearly elucidated in the pig (Rerat, 1978). It seems probable, however, that, in the experimental conditions described, VFA levels are not greatly affected by the dietary cellulose level because a parallel increase in the volume of the cecum takes place as shown in rabbits (Hoover and Heitmann, 1972) and in pigs (R. C. Ewan, Department of Animal Science, Iowa State University, unpublished data). Also, an increase in VFA production may not be reflected in an increase of VFA concentration because the capacity of the cecum and colon for VFA absorption (Argenzio and Whipp, 1979), is much greater than that required in the conditions of this experiment.

The addition of antibiotic (Table 8) resulted in a significant decrease ($P<.01$) in the cecal VFA possibly because

Table 8. Effect of dietary cellulose on cecal VFA concentration, mM

Cellulose level, %	No antibiotic	Antibiotic[a]
Acetate[b]		
2	52.3	40.5
10	47.6	41.6
18	47.8	41.9
Propionate[c]		
2	27.7	18.9
10	29.3	19.4
18	27.4	17.4
Butyrate[d]		
2	11.0[e]	5.2
10	14.4[f]	8.2
18	10.9[e]	7.4
Valerate[g]		
2	2.9[e]	1.1
10	5.0[f]	1.9
18	3.2[e]	1.1

[a]Antibiotic effect, $P<.01$.

[b]Standard error of the difference between two treatment means = $\pm$ 4.5. Standard error of the antibiotic effect = $\pm$ 4.0.

[c]Standard error of the difference between two treatment means = $\pm$ 3.5. Standard error of the antibiotic effect = $\pm$ 2.7.

[d]Standard error of the difference between two treatment means = $\pm$ 1.3. Standard error of the antibiotic effect = $\pm$ 1.5.

[e,f]Values in columns with different subscripts differ, $P<.05$.

[g]Standard error of the difference between two treatment means = $\pm$ 1.7. Standard error of the antibiotic effect = $\pm$ .7.

of changes in the cecal environment as a result of the reduction in fermentation rate (Michel, 1965). A similar effect has been reported by Mason and Just (1976), who showed a significant decrease in fecal VFA in pigs after the administration of neomycin.

The results of this experiment suggest that dry matter and cellulose digestibility are inversely related to dietary cellulose level. There was a maximum daily cellulose digestion capacity of about 35 g/pig for the conditions described. Also, cecal ammonia N was found to have a definite pattern between meals, reaching a maximum 6 hr after feeding. Data for VFA show no effect of dietary cellulose levels on cecal concentrations. The administration of neomycin significantly decreased cecal VFA, increased cecal ammonia and markedly reduced digestion of cellulose.

SECTION IV. EFFECTS OF DIETARY CELLULOSE LEVELS IN INTACT AND CECECTOMIZED PIGS

INTRODUCTION

The chemical composition of dietary fiber is variable, but cellulose generally is the major component. Replacement of 25% dietary starch by cellulose causes a large decrease in the digestibility of the dry matter and a smaller decrease in nitrogen (N) digestibility in the rat (Mason and Palmer, 1973). In the pig, apparent digestibility of N is affected by the nature of the dietary starch (Mason et al., 1976). The effect of increasing cellulose level in typical corn-soybean meal diets on apparent N digestibility, however, has not been clearly elucidated.

Cellulose is digested mainly in the large intestine, and the volatile fatty acids (VFA) produced are absorbed from the cecum and colon of the pig (Cranwell, 1968; Argenzio and Southworth, 1975). The relative importance of cecum and colon in digestive processes of swine has not been established. Lloyd et al., (1958) reported nonsignificant differences between intact and cecectomized pigs, but the few animals involved and the low cellulose content of the diets did not allow definite conclusions. Also, data available in rats (Yang et al., 1969) may not be applicable to the pig because of large species differences in both anatomical structure (Simic and Ilic, 1976) and in rate of passage of digesta (Hecker and Grovum, 1975).

The present study was designed to evaluate the effect

of dietary cellulose upon apparent digestibilities of dry matter, N and cellulose in intact and cecectomized pigs. Plasma urea N (PUN) and plasma cholesterol were measured because their concentrations may be influenced by dietary cellulose (Bodwell, 1975; Story and Kritchevsky, 1978).

MATERIALS AND METHODS

Twelve crossbred, castrated male pigs with an average body weight of 30 kg were housed in smooth-walled pens in an environmentally controlled room. Six pigs were cecectomized by the method described by Lloyd et al. (1958) and allowed to recover for 10 days. Six nonoperated pigs were used as controls. All pigs were fed a basal diet at a level of 3% of body weight daily in two equal feedings (Table 1). The dietary treatments were cellulose (Solka-floc)[1] levels of 2, 10 and 18% of the weight of the basal diet. These amounts were fed in addition to basal diet. Animals were assigned randomly to dietary treatments and to presence or absence of cecum.

During the 40-day experiment, samples were collected every 4th day. Pigs were bled from the anterior vena cava 4 hr after the morning feeding. Plasma was obtained and stored at -20 C until analyzed for PUN by the method of Marsh et al. (1965) and for cholesterol by the method of Searcy and Bergquist (1960). Partial collections of feces were stored in glass jars containing 1N HCl at -20 C until analyzed for dry matter and N by procedures of A.O.A.C. (1975) and for cellulose by detergent fiber method (Van Soest, 1963;

[1]Brown Co., Des Plaines, IL. Chemical composition NDF, 92.5; ADF, 82.1; ADL, 3.0; cellulose, 78.9; hemicellulose, 10.4.

Van Soest and Wine, 1968). Chromium was analyzed by atomic absorption spectrophotometry[1], after wet ashing of samples.

Data were analyzed as a split-plot design. The 3 x 2 factorial combination of dietary cellulose level and presence or absence of cecum were main-plot treatments, and the repeated samplings were subplot treatments. Test of significance for subplot elements was made by using conservative degrees of freedom as described by Geisser and Greenhouse (1958). To reduce the variability associated with individual collections, and for presentation purposes, the experiment was divided into three periods. Values for periods one, two and three are averages of three, four and three chronologically successive collections, respectively.

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[1]Perkin-Elmer, Model 460.

RESULTS AND DISCUSSION

Neither dietary cellulose level, nor presence or absence of cecum affected PUN concentration (Table 9). Because of the high correlation between biological value and PUN (Munchow and Bergner, 1967; Eggum, 1970), PUN is commonly used for evaluation of protein quality (Bodwell, 1975). Urea is synthesized in the liver of ureotelic animals via the urea cycle. Its nitrogen is derived from ammonium ions produced in catabolic processes. Either free ammonia or glutamine can supply these amino groups (Davern and Meselson, 1960; Kornberg, 1969). Also, large intestine ammonia pool and body

Table 9. Effect of dietary cellulose on plasma urea N (mg/dl) of intact and cecetomized growing swine

Days on experiment[a,b]	Cecum	Added cellulose, %					
		2		10		18	
		+	-	+	-	+	-
1-12		12.6	9.8	11.0	11.4	12.2	12.2
13-28		12.2	10.0	11.2	12.6	12.4	13.4
20-40		13.4	10.8	13.0	13.2	13.2	14.6
$\bar{X}$[c]		12.8	10.2	11.8	12.4	12.6	13.4

[a]Average SE .4, n=8.

[b]Linear effect for days on experiment, $P<.01$.

[c]SE .8, n=20.

pool (because ammonia can diffuse freely through the intestinal mucosa; Castell and Moore, 1971) are negatively correlated with dietary cellulose level of swine rations (Farrell and Johnson, 1970; Gargallo and Zimmerman, 1980b). The previous points suggest an inverse relationship between PUN and dietary cellulose level. Our data indicate, however, that an increase in cellulose digestion capability does not appreciably affect PUN concentration. Therefore, it seems that cellulose content of a feedstuff per se would not affect protein quality evaluation of that feedstuff as estimated with PUN.

Concentration of PUN increased ($P<.01$) during the experimental period. This effect was expected because the ratio of energy to protein required by growing swine increases with age (National Research Council, 1979). The increase in PUN level might also have been a response to the increase in apparent N digestibility that occurred during the experiment.

Plasma cholesterol concentrations are presented in Table 10. In spite of variability of data, there was a linear decrease ($P<.05$) in plasma cholesterol as dietary cellulose levels increased. The cecectomized pigs did not show any difference ($P>.10$) for this parameter when compared with the intact pigs, and no appreciable differences ($P>.10$) were found among the three time periods. The decrease in

Table 10. Effect of dietary cellulose on plasma cholesterol (mg/dl) of intact and cecectomized growing swine

Days on experiment[a]	Cecum	Added cellulose, % 2 +	2 -	10 +	10 -	18 +	18 -
1-12		96.7	101.5	108.2	86.0	91.0	90.7
13-28		97.1	98.5	100.5	109.7	95.5	87.1
29-40		109.2	101.7	110.7	89.0	87.0	86.7
$\bar{X}$[b,c]		101.0	100.6	106.5	94.9	91.2	88.2

[a]Average SE 6.0, n=8.

[b]SE 3.5, n=20.

[c]Linear effect for added cellulose, $P<.05$.

plasma cholesterol associated with high fiber diets has been well-documented (Story and Kritchevsky, 1978; Stasse-Wolthuis et al., 1979). The fraction of dietary fiber responsible for this effect has not been clearly defined. Lignin and pectin form unabsorbable complexes with cholesterol in the intestinal lumen (Leveille and Sauberlich, 1966; Leitzmann et al., 1979). The extent of microbial fermentation probably does not have a significant effect on cholesterol turnover because it takes place in the post-absorptive regions of the gut (Drasar and Hill, 1974). In our study, lignin concentrations of the three experimental diets (.9, 1.3 and 1.7% of dry matter, respectively) were much lower than those reported as effective in reducing

plasma cholesterol in rats (Leitzmann et al., 1979). Therefore, data in Table 3 suggest that high levels of dietary cellulose per se affect plasma cholesterol concentration in growing swine.

Apparent dry matter digestibility coefficients (Table 11) were similar to those reported in the literature for pigs fed similar diets (Farrell and Johnson, 1970; Farrell, 1973). This parameter decreased ($P<.01$) as dietary cellulose increased, but it was not affected by the absence of the cecum. Our results support the previous observations of Lloyd et al. (1958) that cecectomy does not decrease digestive capacity of the pig to any great extent. Dry matter digestibility increased during the experiment in all pigs. The increase in

Table 11. Effect of dietary cellulose on apparent dry matter digestibility (%) of intact and cecectomized growing swine

Days on experiment[a,b]	Cecum	Added cellulose, %					
		2		10		18	
		+	-	+	-	+	-
1-12		81.1	80.9	73.3	74.3	66.3	69.1
13-28		84.0	84.0	77.7	78.0	71.9	72.3
29-40		84.8	83.1	78.7	80.3	74.1	75.6
$\bar{X}$[c,d]		83.3	82.7	76.6	77.5	70.8	72.3

[a]Average SE .9, n=8.

[b]Linear effect for days on experiment, $P<.01$.

[c]SE .6, n=20.

[d]Linear effect for added cellulose, $P<.01$.

digestibility can be explained by the changes in apparent N and cellulose digestibilities.

The increase in dietary cellulose level resulted in a significant linear decrease ($P<.01$) of percentage cellulose digestibility. The values (Table 12) are very similar to those found previously in a similar experiment (Gargallo and Zimmerman, 1980b), but there is no uniformity in the literature for the relationship between dietary cellulose and its digestibility. Keys et al. (1970), feeding orchardgrass, and Farrell (1973), feeding purified cellulose, found them unrelated. Later reports of King and Taverner (1975), Schneider and Kirchgessner (1977), using a variety of feedstuffs, and Kass et al. (1980a), with alfalfa meal, indicated a relationship similar to the one shown by our data.

The pigs receiving the high level and, possibly, those receiving the intermediate level of dietary cellulose may not have reached a maximum cellulose digestion capability when the experiment ended. Only the lowest cellulose intake group stabilized after 20 days on experiment, but no significant interactions between dietary cellulose level and time were found. Henry and Etienne (1969) reported a slight increase in cellulose digestibility related to an increase in body weight. It seems unlikely that body weight is the only cause of the increase in cellulose digestion in this experiment because the pattern of increase was not uniform for pigs fed the

Table 12. Effect of dietary cellulose on apparent cellulose digestibility (%) of intact and cecectomized growing swine

Days on experiment[a,b]	Cecum	Added cellulose, % 2 +	2 -	10 +	10 -	18 +	18 -
1-12		22.2	19.5	16.6	11.4	10.7	11.8
13-28		30.7	33.3	24.0	19.5	18.3	17.0
29-49		37.7	34.8	38.7	37.5	25.6	24.1
$\bar{X}$[c,d]		30.2	29.2	26.4	22.8	18.2	17.6

[a]Average SE 4.3, n=8.

[b]Linear effect for days on experiment, $P<.01$.

[c]SE 5.0, n=20.

[d]Linear effect for added cellulose, $P<.05$.

three experimental diets. The results of our study support the hypothesis of Cunningham et al. (1962) that pigs receiving large amounts of fiber for a long period adapt by digesting increasing amounts of complex carbohydrates. The mechanisms by which adaptation is accomplished have not been studied. Possibly, a progressive distention of the gut by pigs fed a high cellulose diet (R. C. Ewan, unpublished data) decreases the rate of passage of digesta through the tract. As a result, an intestinal flora with a longer generation time develops (Stouthamer and Bettenhaussen, 1973), and, also, a more prolonged microbial attack on the cellulose

takes place. One or more of these factors may account for the increase in cellulose digestion shown by the pigs.

The group receiving the lowest level of dietary cellulose digested less ($P<.10$) cellulose (Table 13) than did the other two groups, which showed no difference between them. It seems, in accordance with our previous findings (Gargallo and Zimmerman, 1980b), that, beyond a certain level at which maximal gut distension is attained and, consequently, the rate of passage is increased, further additions of cellulose to the diet do not result in an increase in total cellulose digestion capability. At the end of the experiment, pigs had a maximum daily rate of cellulose digestion of about 135 g per 100 kg of body weight. Also, removal of the cecum

Table 13. Effect of dietary cellulose on total cellulose digestion (g/100 kg body weight daily) of intact and cecectomized growing swine

Days on experiment[a,b]	Cecum	Added cellulose, %					
		2		10		18	
		+	-	+	-	+	-
1-12		32.5	28.5	57.2	39.0	56.8	62.7
13-28		44.9	48.7	82.5	66.9	97.2	90.3
29-40		55.1	50.9	132.9	128.9	135.8	127.9
$\bar{X}$[c,d]		44.2	42.7	90.9	78.3	96.6	93.6

[a]Average SE 14.3, n=8.

[b]Linear effect for days on experiment, $P<.01$.

[c]SE 15.7, n=20.

[d]Comparison of 2 vs. 10 and 18% added cellulose, $P<.10$.

resulted in a slight but consistent decrease in cellulose digestion, even though the differences were not significant.

An increase in dietary cellulose reduced (P<.01) apparent N digestibility (Table 14). This effect may be partly related to an increase in intestinal desquamation (Bergner et al., 1975), but the main cause is the increase in fecal N loss of metabolic origin (Mason et al., 1976), largely represented by microbial protein. In our experiment, a significant negative correlation (r = -.93, P<.01) was found between total cellulose digested daily and apparent N digestibility for the six overall treatment (diet x cecum)

Table 14. Effect of dietary cellulose on apparent N digestibility (%) of intact and cecectomized growing swine

Days on experiment[a,b]	Cecum	Added cellulose, %					
		2		10		18	
		+	-	+	-	+	-
1-12		75.6	76.5	68.3	72.7	64.1	67.3
13-28		78.2	79.6	75.2	76.7	70.8	73.0
20-40		79.5	78.0	74.3	78.3	74.7	77.4
$\bar{X}$[c,d,e]		77.8	78.0	72.6	75.9	69.9	72.6

[a]Average SE 1.3, n=8.

[b]Linear effect for days on experiment, P<.01.

[c]SE .9, n=20.

[d]Linear effect for added cellulose, P<.01.

[e]Cecum effect, P<.05.

means. Although this experiment did not allow determination of the cause of this negative correlation, the results suggest that, as it happens in the rat (Mason and Palmer, 1973), the extent of fermentation in the large intestine of the pig has an effect on the amount of fecal nitrogen excreted.

As occurred for the rest of the dietary components, apparent N digestibility increased during the experiment. At the end, pigs receiving the intermediate and high levels of dietary cellulose showed similar apparent N digestibility coefficients. Figure 4 describes graphically the relationship between total cellulose digested daily and apparent N digestibility within each time period. The progressively less negative slopes of the three lines (.16, .03 and .01, $P<.05$) represent the adaptation phenomenon. This change in the slopes indicates that the negative effect of increasing levels of cellulose digested daily on apparent N digestibility decreased with each successive experimental period.

Kondra et al. (1974) demonstrated an increase in weight of digestive tract and in the height of intestinal villi when high fiber diets were fed to chickens. These authors concluded that poultry species are capable of anatomical and physiological adaptation to nutrient concentration of the diet. These mechanisms, although not documented in swine, may be involved in the increased efficiency of N digestion with

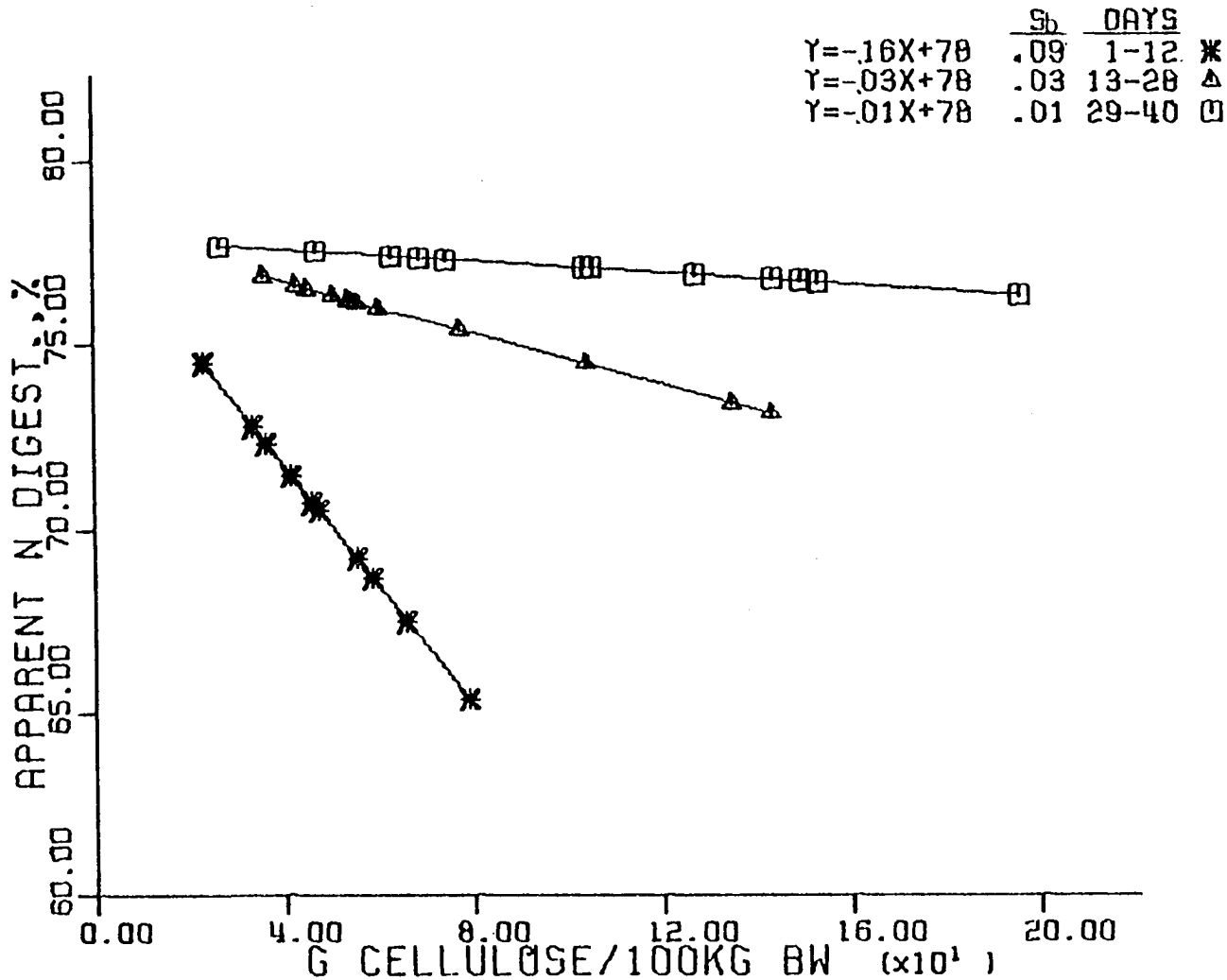

Figure 4. Effect of adaptation to increasing levels of dietary cellulose on the relationship between apparent N digestibility and daily cellulose digestion (Sb = standard deviation of regression coefficient)

time shown by the experimental pigs. Also, a gradual increase in the time of retention of digesta and possible changes in microbial flora in the pigs could combine with intestinal anatomical modifications resulting in a more efficient N absorption and decrease in excretion of microbial protein.

Cecectomized pigs seemed to digest more N than did the intact pigs ($P<.05$). This response can be explained in terms of a reduction of metabolic fecal N, resulting from less cellulose digested by cecectomized pigs (Smith, 1961; Mason, 1969). Apparent N digestibility was a less variable parameter than cellulose digestibility (coefficients of variation, 1.2 vs. 20.5%, respectively), and consequently, it was a more sensitive measurement. The high variability in cellulose digestibility explains the lack of statistical significance ($P>.10$) of the lower cellulose digestion associated with cecectomy. Therefore, these data indicate that absence of a cecum altered cellulose and N apparent digestibility, but effects were of relatively small magnitude.

The results of this experiment suggest that dry matter, N and cellulose apparent digestibility are inversely related to dietary cellulose level. There was a maximum daily cellulose digestion of about 135 g/100 kg body weight for the conditions described. Also, adaptations by pigs to compensate for the presence of cellulose in the diet were evident.

Cecectomy produced a slight decrease in cellulose digestibility and a consequent increase in apparent N digestibility. These changes, however, were relatively small, and cecectomy did not significantly affect overall digestion capabilities of pigs.

SECTION V. EFFECT OF SUNFLOWER HULLS ON LARGE INTESTINE FUNCTIONALITY IN FINISHING SWINE

INTRODUCTION

In pigs, dietary fiber is digested mainly in the large intestine by anaerobic microbial fermentation, and the volatile fatty acids (VFA) produced are absorbed from cecum and colon (Cranwell, 1968; Argenzio and Southworth, 1975). There is no agreement in the literature, however, on production rate and subsequent energy utilization of VFA (Friend et al., 1964; Farrell and Johnson, 1970; Imoto and Namioka, 1978). Therefore, with present knowledge, it is difficult to predict the nutritional value of specific fiber sources.

Production of sunflower has increased almost threefold since 1977 in the United States (Crop Production, 1979). Because of the present incorporation of sunflower seed meal with hulls and, occasionally, of sunflower hulls (SFH) alone in the diet of nonruminant animals, additional information about the nutritional value of SFH for these species is needed.

The objectives of our study were 1) to estimate the effect of dietary SFH upon VFA concentration and production rate in cecum and colon, and 2) to evaluate the amount of VFA energy, as percentage of net maintenance energy requirement, derived from fermentation taking place in cecum and colon. Plasma urea nitrogen (PUN) and plasma glucose (PG) were measured because their concentrations may be affected

by nutrient availability (Bodwell, 1975) and VFA production rate (Jordan and Phillips, 1978).

MATERIALS AND METHODS

Twenty-four crossbred pigs in eight litters with an average body weight (BW) of 67 kg were housed in individual slatted-floor pens. They were randomly allotted from outcome groups of sex within litter to three dietary treatments. All pigs were fed a basal diet at a level of 3% of BW daily in one evening feeding (Table 1). The dietary treatments were finely ground SFH[1] levels of 2, 10 and 20% of the weight of the basal diet. These amounts were fed in addition to basal diet.

At 95 kg body weight, pigs were slaughtered 10 hr after feeding. At slaughter, a blood sample was taken, and the intestinal tract collected. The tract was divided by ligature into small intestine, cecum and colon. About 250 g of digesta was taken from both cecum and apex of the spiral coil of colon for measurement of VFA production rates. The rest of digesta in cecum and colon was then collected and weighed separately. The empty weight of each intestinal segment also was recorded.

VFA production rates were measured by a short-term *in vitro* fermentation method described by Stewart *et al.* (1958). Samples were placed in a preweighed, warmed glass jar, gassed

[1]SFH chemical composition (%): NDF, 70.6; ADF, 53.0; ADL, 15.3; cellulose, 37.7; hemicellulose, 17.6.

with carbon dioxide, stoppered and incubated in a water bath at 39 C for 60 minutes. Sub-samples of about 50 ml were obtained at 0, 30 and 60 min of incubation, bacterial fermentation was stoppered by adding 1 ml 12N H_2SO_4, and sub-samples were stored at -20 C until processed for chemical analysis. VFA production rates were determined as the slope of the increase in VFA concentrations during incubation (Stewart et al., 1958).

PUN was analyzed by the method of Marsh et al. (1965), and PG by an enzymatic colorimetric method.[1] VFA were measured by gas chromatography by using a Perkin-Elmer 900 equipped with a column packed with SP-1200/H_3PO_4 on Chromosorb W AW.[2] Amyl alcohol was used as the internal standard.

Results were analyzed statistically by analysis of variance using a randomized complete-block model. Intestinal fill weight and empty intestinal weight were analyzed by using body weight as a covariant (Snedecor and Cochran, 1967).

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[1]Sigma Chemical Co., St. Louis, MO. Technical Bulletin No. 510.

[2]Supelco, Inc., Bellefonte, PA. Bulletin 749A.

RESULTS AND DISCUSSION

PUN concentration was lower (P<.05) for pigs fed the highest level of SFH than for those fed the other two dietary levels (Table 15). Because the protein in SFH is essentially undigestible (National Research Council, 1971) the three experimental diets can be considered of identical digestible protein content. These data do not agree with the results of previous experiments (Gargallo and Zimmerman, 1980b), in which, there were no significant differences in PUN among pigs fed 2, 10 and 18% purified cellulose.

In spite of the large variability encountered, PG tended to be higher (P<.10) for pigs fed the highest level of SFH than for those fed the other two levels (Table 15). Also,

Table 15. Effect of dietary SFH on plasma urea N, plasma glucose and empty intestinal weight

Added SFH, %	PUN[a,b] mg/dl	PG[a,c] mg/dl	Empty weight, g		
			SI	Cecum	Colon
2	11.1	98.0	1243	135	1050
10	11.5	95.4	1457	136	1103
20	10.1	111.1	1253	134	1109
SE	.5	7.6	56	8	54

[a] $R = -.34$, $P<.10$.

[b] Comparison of 2 and 10 vs. 20% added cellulose, P<.05.

[c] Comparison of 2 and 10 vs. 20% added cellulose, P<.10.

a marginally significant correlation ($r = -.34$, $P < .10$) was found between PUN and PG. The cause for the responses described and the possible interrelationship between PUN and PG could not be identified in this experiment.

The increasing levels of SFH in the diet did not have any detectable effect either on average daily gain (ADG: 543, 487 and 515 g for the 2, 10 and 20% SFH diets, respectively) or on empty intestinal weight (Table 15). The effect of dietary fiber upon empty intestinal weight is not clear from reports in the literature. In general, when significant differences in ADG were present among experimental diets, dietary fiber had an effect on empty intestinal weight (Bohman et al., 1955; Kass et al., 1980a). In experiments similar to ours, however, in which no differences in ADG were observed (Hochstetler et al., 1959; Cunningham et al., 1961), dietary fiber did not have any effect on empty intestinal weight. It seems possible, because animals were slaughtered at constant weight in all reports cited, that age, stage of development and body condition, rather than dietary fiber, were responsible for differences in empty intestinal weight.

Dry matter (DM) content of digesta showed a linear increase in cecum ($P < .05$) and colon ($P < .01$) with the addition of SFH to diets (Table 16). The increased feed intake associated with treatments could alter the dry matter content

Table 16. Effect of dietary SFH on DM content and weight of cecum and colon fill

Added SFH, %	Dry matter, %		Fill weight, g			
			Wet		Dry matter	
	Cecum[a]	Colon[b]	Cecum	Colon	Cecum	Colon
2	16.0	19.7	368	952	60	190
10	17.1	22.5	290	949	48	210
20	18.1	24.4	319	865	55	204
SE	.5	.7	48	90	8	18

[a]Linear effect for added SFH, $P<.05$.

[b]Linear effect for added SFH, $P<.01$.

of digesta, but our experiment was not designed to determine this effect. Fine grinding of fiber has been reported to reduce fecal water (Van Soest et al., 1978). The addition of SFH to the basal diet resulted in diets of fine consistency, which could be partly responsible for the effect observed. Also, it is generally accepted that each fiber source, because of its physical and chemical properties, is unique and therefore, has an effect upon digesta and fecal DM content (Van Soest et al., 1978; Van Soest, 1975). In spite of the change in DM, no treatment differences were observed for intestinal fill weight, either on wet or dry basis (Table 16).

Microbial breakdown of carbohydrates results in formation

of organic acids, mainly VFA and carbonic acid (Michel, 1961; Hall, 1965). In the pig, VFA concentrations are high in the large intestine and relatively low in the rest of the digestive tract (Argenzio and Southworth, 1975). VFA concentrations in cecum and colon before incubation are shown graphically in Figures 5 and 6, respectively. Mean total VFA concentrations (acetate + propionate + butyrate) were lower than reported in experiments using purified cellulose (DeBarthe and Kane, 1980; Gargallo and Zimmerman, 1980b) and higher than those obtained with alfalfa meal diets (Kass et al., 1980b). Also, mean total VFA concentrations were higher in cecum than in colon ($P<.05$). Data are expressed on dry matter basis to obviate differences in hydration capacity between experimental diets.

Acetate concentration was not affected by the addition of SFH to the diet, either in cecum (Figure 5) or in colon (Figure 6). Propionate and butyrate concentrations decreased linearly in cecum ($P<.05$) and colon ($P<.01$) with increased dietary SFH. These decreases in overall VFA concentrations in cecum and colon of pigs, when natural fiber sources are fed, have been reported by others (Friend et al., 1963; Argenzio and Southworth, 1975; Kass et al., 1980b), and they are attributed mainly to an increase in the rate of passage of digesta through the intestinal tract (Argenzio and Southworth, 1975). However, this effect was not observed when

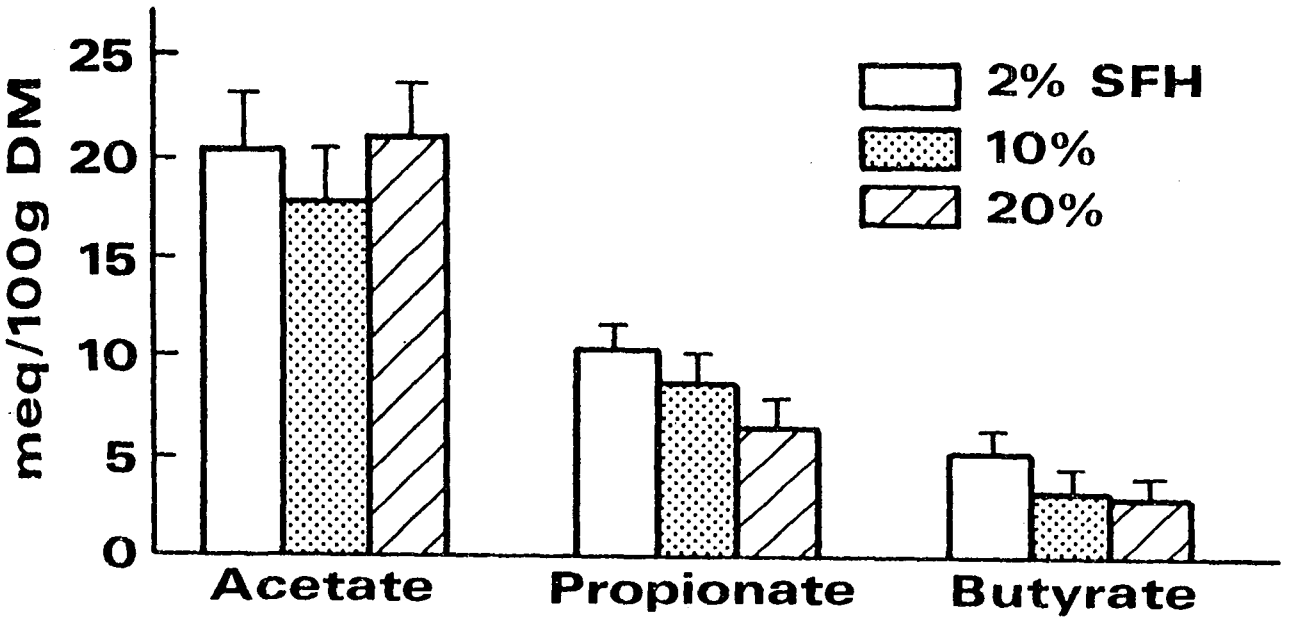

Figure 5. Effect of dietary SFH on cecum VFA concentrations (+ SE)

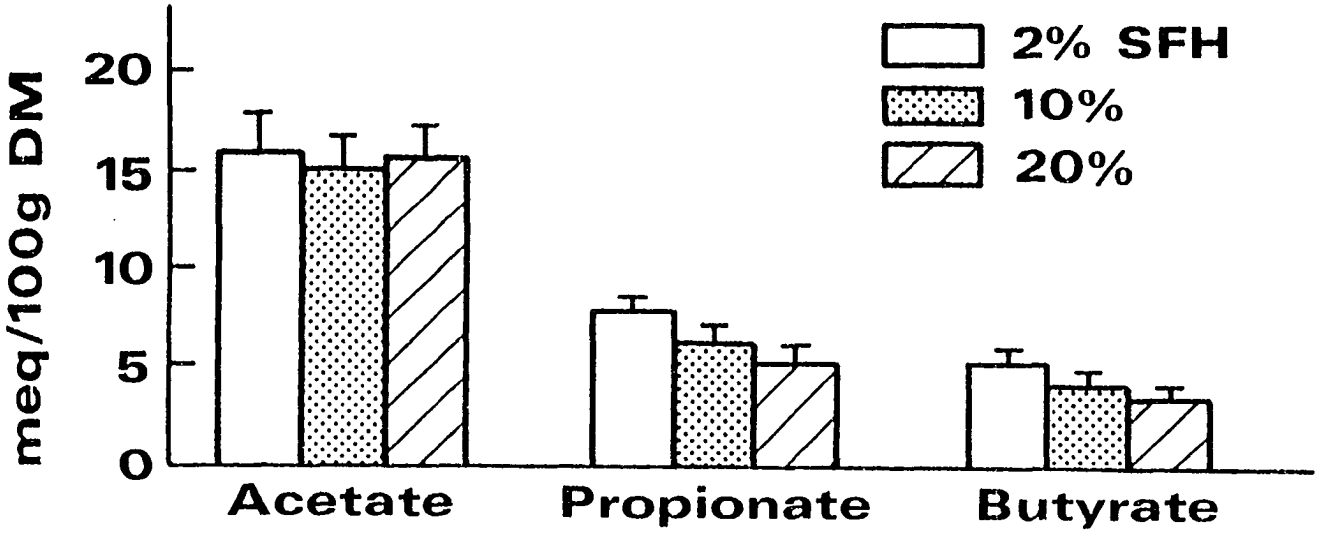

Figure 6. Effect of dietary SFH on colon VFA concentrations (+ SE)

purified cellulose was fed (Farrell and Johnson, 1970; Gargallo and Zimmerman, 1980b).

The VFA concentration changes observed in our experiment with increasing dietary SFH altered the relative concentrations of acetate, propionate and butyrate in cecum (Figure 7) and colon (Figure 8). Relative acetate concentration (meq of acetate/100 meq total VFA) increased linearly ($P<.05$) with SFH additions to the diet, whereas relative concentrations of propionate and butyrate decreased linearly ($P<.05$). This effect of dietary fiber on relative VFA concentrations is not completely understood, but it has been observed repeatedly in ruminants (Bauman et al., 1971) and in pigs (Friend et al., 1963; Kass et al., 1980b) when natural fiber sources were used. Other experiments in which purified cellulose was fed, however, showed no effect (Farrell and Johnson, 1970; Gargallo and Zimmerman, 1980b) or an opposite effect (DeBarthe and Kane, 1980).

No significant differences were found between VFA production rates in cecum (Figure 9) or colon (Figure 10). Production rate of colon propionate showed a linear decrease ($P<.05$) with increased dietary SFH. Production rates of cecum propionate and butyrate and colon acetate also showed a trend towards a decrease, but these differences did not approach statistical significance ($P>.10$). Farrell and Johnson (1972) found a decrease in VFA production rates in

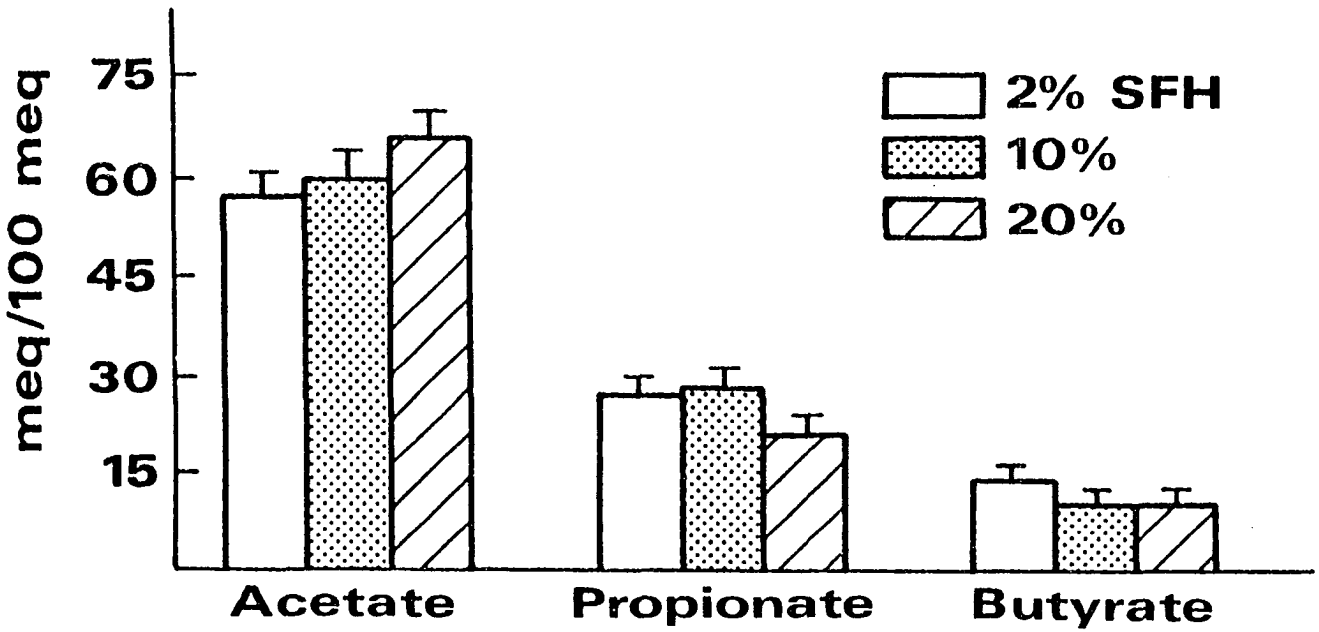

Figure 7. Effect of dietary SFH on cecum relative VFA concentrations (+ SE)

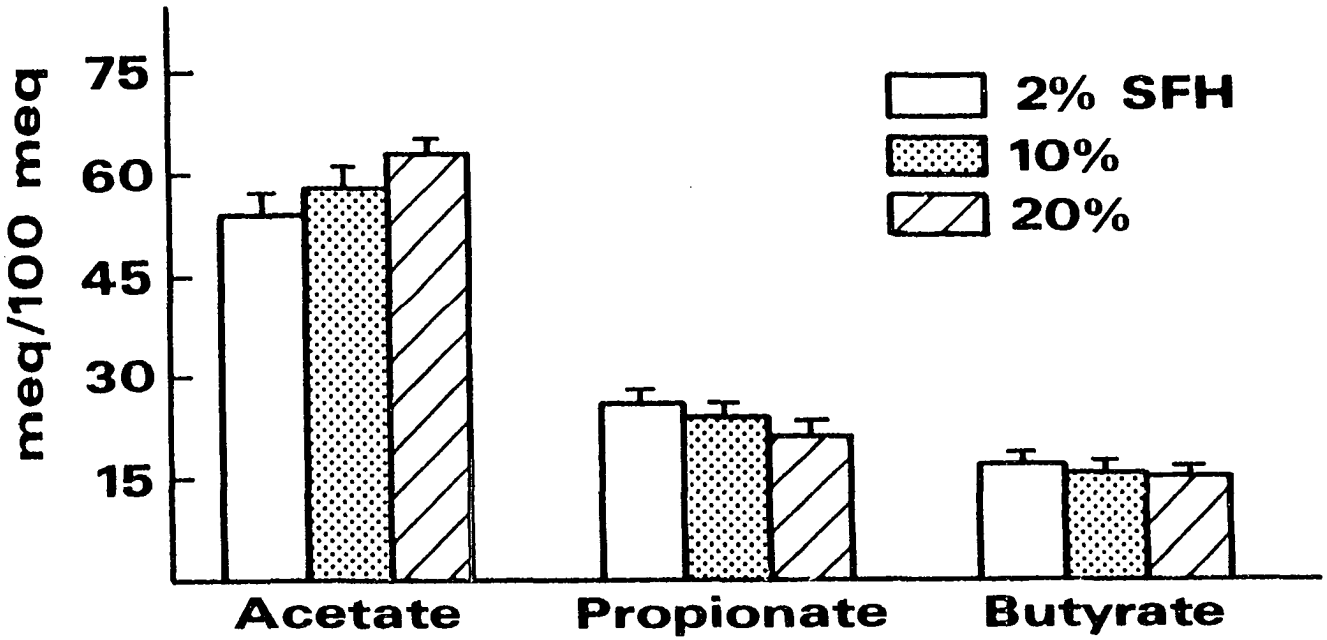

Figure 8. Effect of dietary SFH on colon relative VFA concentrations (+ SE)

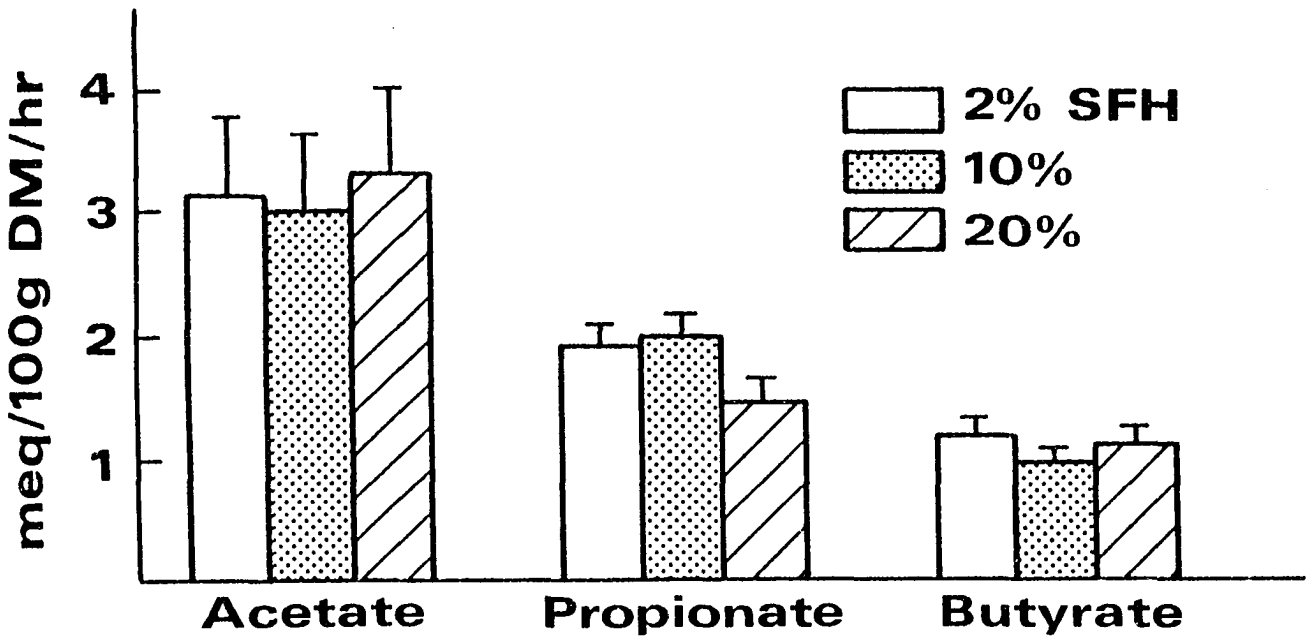

Figure 9. Effect of dietary SFH on cecum VFA production rates (+ SE)

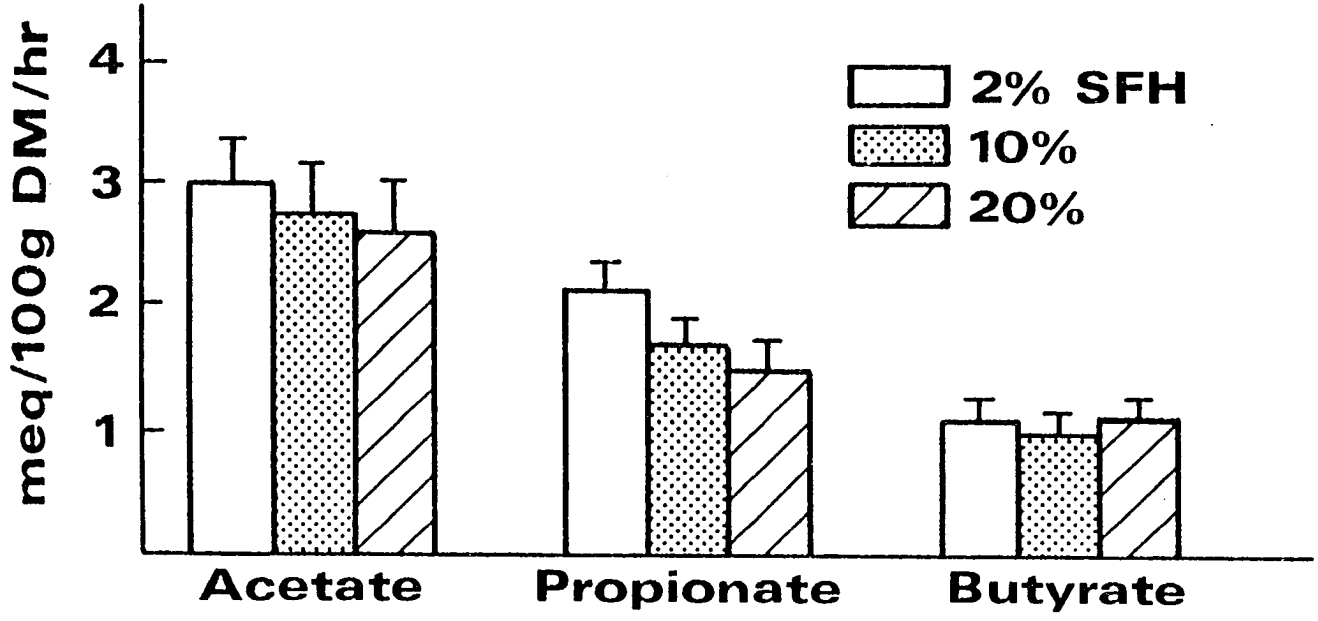

Figure 10. Effect of dietary SFH on colon VFA production rates (+ SE)

cecum of pigs by increasing dietary cellulose from 8 to 26%, although the VFA production rates that they reported were higher than the ones found in our experiment. Our data, along with those of other reports (Farrell and Johnson, 1970; Imoto and Namioka, 1978; Kass et al., 1980b), suggest that the increase in VFA production observed in pigs when some fiber sources are fed is the result of an increase in the amount of digesta present in the large intestine rather than of an increase in VFA production rates.

Total daily VFA production in the cecum and colon was estimated by multiplying the production rates by the weight of digesta in these sections of the intestine and by 24 hours. It was assumed that VFA production rates 10 hr after feeding are good estimates of average daily production rates because pigs were fed once daily. On the basis of gross caloric values of 3.48, 4.71 and 5.92 kcal/g for acetate, propionate and butyrate (Handbook of Chemistry and Physics, 1968), the energy produced daily in cecum and colon in the form of VFA amounted, as an average, to 135, 120 and 110 kcal for pigs weighing 95 kg and fed diets containing 2, 10 and 20% SFH, respectively. Net maintenance energy required was considered to be 71 kcal/$kg^{.75}$ (Ewan, 1976). VFA energy produced daily in cecum and colon represented 6.2, 5.6 and 5.0% of net maintenance energy requirement of 95-kg pigs fed diets containing 2, 10 and 20% SFH, respectively. The fraction

of this energy that is available to the pig could not be determined in this experiment because a rather large amount of these acids is metabolized during their passage through the mucosa (Ly, 1974) and because rectal VFA production and fecal VFA excretion were not measured.

The results of our experiment indicate that fiber present in SFH did not greatly affect the extent of fermentation taking place in the large intestine, as measured by total VFA production. Therefore, it was concluded that fiber present in SFH essentially is not utilized by finishing swine.

SUMMARY

A T-cannula was designed for placement in the gastro-intestinal tract of pigs used for nutritional studies. It was made from available and inexpensive polyvinylchloride plumbing fittings. The main advantages of the cannula are light weight, good tolerance by the animals, short projection from the body wall, simplicity of construction and patency for several months.

Four trials were conducted to study the characteristics, limiting factors and nutritional implications of dietary fiber digestion in the large intestine of the growing pig. In all cases, a 16% crude protein corn-soybean meal diet was used as a basal (Table 1). When pertinent, additions, by weight of basal diet, of either purified cellulose (solka-floc) or sunflower hulls (SFH) were made. In trial 1, lactic casein and corn starch were infused into the terminal ileum to study some aspects of large intestine fermentation. Trial 2 was designed to measure the digestibility of purified cellulose and its influence on large intestine fermentation. In trial 3, digestibility of cellulose and its effects on apparent nitrogen (N) digestibility were further investigated. In trial 4, the fermentative capacity and the nutritive value of fiber present in sunflower meal were determined.

About 15% of dry matter present in the basal diet

disappeared in the large intestine (Table 2), indicating a significant role of the large intestine in digestion. Ten percent of dietary starch escaped digestion in the small intestine and it was completely digested in the large intestine (Table 2). An amount equivalent to 26% of dietary N (it may not have been of dietary origin) reached the terminal ileum. This N showed a rather poor apparent digestibility (29%) in the large bowel. Dietary total protein (amino acids) showed an even lower apparent digestibility (20%) than N (Table 20). These low digestibilities of nitrogenous compounds in the large intestine result because of active synthesis of microbial protein. Microbial protein synthesized in the large intestine is essentially nonutilizable by the pig and it is voided in the feces.

The addition of purified cellulose to the basal diet resulted in a linear decrease ($P<.01$) in apparent cellulose digestibility. Coefficients ranged from 30 to 42% when 2% cellulose was added to the basal diet and from 10 to 18% with the addition of 18% cellulose. These values are overall means of trials 2 and 3, Tables 7 and 12. Total cellulose digestion capacity, however, reached a maximum of about 135 g/100 kg body weight daily with the addition of 10% cellulose to the basal diet. Further addition of dietary cellulose did not result in increased cellulose digestion (Table 13). The administration of 150 mg/kg body weight of neomycin sulfate completely abolished cellulose digestion, regardless of dietary

level of cellulose (Table 7). This result confirms the bacterial origin of cellulose digestion. Starch fermentation in the large intestine was much more efficient than cellulose digestion. Pigs of 40 kg body weight were able to digest at least 150 g corn starch, infused daily into the terminal ileum, whereas they only digested approximately 50 g of dietary cellulose daily.

Cecal volatile fatty acid (VFA) concentrations were not affected by the addition of purified cellulose to the basal diet (Table 8). The administration of neomycin resulted in a decrease ($P<.01$) in concentrations of all VFA in the cecum (Table 8). Additions of SFH decreased propionate and butyrate concentrations in cecum ($P<.05$) and colon ($P<.01$) but acetate concentration was not significantly affected in either the cecum or colon (Figures 5 and 6). Changes in concentrations of VFA with increasing dietary SFH altered the relative proportions of acetate, propionate and butyrate in cecum (Figure 7) and colon (Figure 8). Relative acetate concentration (meq of acetate/100 meq total VFA) increased linearly ($P<.05$) with SFH additions to the diet, whereas propionate and butyrate concentrations decreased linearly ($P<.05$). These changes occurred only with SFH additions to the basal diet. The addition of purified cellulose did not alter relative VFA concentrations (Table 8). VFA production rates in cecum

(Figure 9) and colon (Figure 10) showed decreasing trends with SFH additions to the diet, but these trends were not statistically significant, except for colon propionate (linear decrease, $P<.05$). The gross energy of VFA produced daily in cecum and colon represented 6.2, 5.6 and 5.0% of net energy of maintenance of 95-kg pigs fed diets containing 2, 10 and 20% SFH, respectively. Therefore, it seems that fiber in SFH is not utilized by finishing swine.

The microflora in the large intestine of 40-kg pigs completely digested the 60 g of lactic casein infused daily into the terminal ileum. Nitrogen contained in casein was either retained or appeared in the urine as urea (Table 3). The high correlation ($r = .82$, $P<.01$) between urinary urea N and urinary orotic acid suggests that an increase in urea cycle activity and the consequent increase in urinary urea excretion occurred when casein was infused. When corn starch was infused, there was an increase ($P<.05$) in fecal N excretion (Table 3). This N was totally accounted for by the increase in fecal total protein (Table 4). The ratio RNA N: total protein N obtained in feces was .128 $\pm$ .013. The similarity of this ratio to that of the microbial population in the rumen indicated that, in pigs fed the basal diet and infused with casein and/or corn starch, fecal total protein was all of microbial origin. Therefore, from data in Table 4 it was calculated that digestion of 100 g of corn starch in

the large intestine of the pig increased fecal microbial protein by 5.2 grams. The increase in fecal microbial protein resulting from starch infusion indicates that energy is usually the limiting factor for microbial growth in the large intestine. Conversely, N was not limiting because infusion of casein did not result in a significant increase in fecal total protein.

An increase in dietary cellulose reduced ($P<.01$) apparent N digestibility (Table 14). If the microbial yield of cellulose fermentation is similar to the yield of starch fermentation described previously, the negative relationship between cellulose digestion and apparent N digestibility observed during the last period of trial 3 (Figure 4) could be explained entirely by an increase in fecal microbial protein.

Cecal ammonia N concentration seemed to be lower in pigs digesting larger amounts of cellulose than in pigs with less fermentative activity in the large intestine, but the difference was not statistically significant (Table 13). A large increase ($P<.01$) in cecal ammonia N was observed when cellulose digestion was arrested by administering neomycin (Table 13). Consequently, cecal ammonia N concentration was somewhat dependent upon fermentation rate, although other factors may influence this parameter.

Plasma urea N (PUN) concentrations were measured in all

trials (Tables 5, 6, 9 and 15). No treatment differences were observed for this parameter, except for an increase ($P<.05$) when casein and starch were infused together and a decrease ($P<.05$) when 20% SFH was added to basal diet. Differences in PUN concentration between dietary carbohydrate treatments, if present, were of much smaller magnitude than differences brought about by the protein fraction of the diet. Therefore, it seems that events taking place in the large intestine leading to fermentative digestion did not affect PUN to a significant extent.

Differences between intact and cecectomized pigs in apparent dry matter (Table 11), cellulose (Table 12) and N ($P<.05$, Table 14) digestibilities were small, and cecectomy did not affect significantly the overall digestion capabilities of pigs. This capacity of the colon to take over cecal function can be partially explained because the dry matter content in the colon of a 90-kg pig is about four times larger than in cecum (Table 16). Thus, the colon represents a substantially larger fermentation chamber than the cecum.

A definite digestive adaptation to increasing levels of dietary cellulose was found within the experimental period. Apparent dry matter (Table 11), cellulose (Table 12) and N (Table 14) digestibilities increased linearly ($P<.01$) over a 40-day period. Figure 4 describes graphically the change in

the relationship between total cellulose digested daily and apparent N digestibility with time. At the beginning of the experiment, the reduction in apparent N digestibility resulting from an increase in cellulose digestion was larger than could be accounted for by the increase in fecal bacterial nitrogen. The negative effects of increasing levels of cellulose digested daily on apparent N digestibility decreased gradually throughout the experimental period. At the end of the 40-day experiment, microbial protein synthesis in the large intestine could account for the entire decrease in apparent N digestibility observed when cellulose digestion increased.

The results described suggest that the growing pig is able to digest considerable amounts of dietary fiber in the large intestine. The great variability in chemical composition of dietary fibers does not allow, at the present time, a prediction of their nutritional value. Therefore, effort should be devoted to determine the anatomical, physical and chemical interrelationships between different plant fiber fractions. As a result of that research, a model could be developed to predict digestibility of plant fiber sources from their physical and chemical characteristics.

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APPENDIX A: ANALYSIS OF VARIANCE OF VARIABLES IN SECTION II

Table A1. Analysis of variance of average daily gain, plasma urea N, urinary orotic acid, fecal total protein and fecal RNA

Source of variation	d.f.	Mean squares: Average daily gain, g	Plasma urea N, mg/dl	Urinary orotic acid, g/2 days	Fecal total protein g/2 days	Fecal RNA, g/2 day
Period	3	282635***	1.7	58.6	584.4	12.1
Pig	7	11164	17.1***	35.3	559.8	14.2
Period x pig	21	15076	1.8	23.9	277.7	4.9
Treatment	3	16877	3.6	31.2	465.1	5.5
Casein	1	22062	3.6	28.9	64.2	0.0
Starch	1	26396	.9	45.1	1274.4**	16.7*
Casein x starch	1	2173	6.5**	19.8	56.8	0.0
Residual	18	14776	1.5	22.7	246.5	4.8

*P<.10.

**P<.05.

***P<.01.

Table A2. Analysis of variance of N retention, N excretion and fecal N

Source of variation	d.f.	Mean squares			
		N retention, g/2 days	N excretion, g/2 days	Fecal N	
				g/2 days	% of excretion
Period	3	14.5	497.8***	58.7***	10.3
Pig	7	167.9	142.9	28.8**	181.1**
Period x pig	21	95.6	74.5	8.3	87.3
Treatment	3	294.0	134.7	15.8	123.4
Casein	1	786.8**	353.7**	14.6	62.5
Starch	1	86.7	34.3	30.9**	295.1**
Casein x starch	1	8.4	16.3	2.0	12.6
Residual	18	62.5	64.4	7.0	57.7

**P<.05.

***P<.01.

Table A3. Analysis of variance of urinary N, urinary urea N and urinary ammonia N

Source of variation	d.f.	Mean squares				
		Urinary N		Unaccounted urinary N, g/2 days	Urinary urea N, g/2 days	Urinary ammonia N, g/2 days
		g/2 days	% of excretion			
Period	3	216.7*	10.3	18.0	132.1*	.6
Pig	7	164.7*	181.1**	6.5	106.6*	.7
Period x pig	21	77.4	67.1	7.9	52.6	.8
Treatment	3	128.2	123.4	3.4	147.8*	1.1
Casein	1	224.2*	62.5	6.5	294.3**	2.3
Starch	1	130.4	295.1**	0.0	134.8*	.7
Casein x starch	1	29.9	12.6	3.9	14.5	.2
Residual	18	68.9	57.7	8.7	36.9	.8

*P<.10.

**P<.05.

APPENDIX B: STATISTICAL ANALYSIS OF VARIABLES IN SECTION III

Table B1. Analysis of variance of plasma urea N, apparent dry matter and cellulose digestibility[a]

Source of variation	d.f.[b]	Mean squares		
		Plasma urea N, mg/dl	Apparent dry matter digestibility, %	Apparent cellulose digestibility, %
Diet	2	.5	931.2***	3907.8***
Linear	1	-	1340.4***	4645.7***
Quadratic	1	-	522.0***	3169.8***
Rep (diet)	3	81.7	15.4	198.2
Period	11 (1)	4.1	27.4	707.9
1-10 vs. 11-12	1	.1	12.9	6029.2***
Diet x period	22 (2)	2.2	29.9	451.2
Remainder	33 (3)	3.7	15.6	378.1

[a]Tests of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

***P<.01.

Table B2. Analysis of variance of cecal ammonia N and cecal VFA[a]

Source of variation	d.f.[b]	Mean squares				
		Cecal ammonia N, mg/dl	Cecal VFA, mM			
			Acetate	Propionate	Butyrate	Valerate
Diet	2	66.0	533.0	103.6	334.1**	106.2**
1+3 vs. 2	1	-	-	-	432.7**	195.3**
Rep (diet)	3	142.5	248.8	149.3	22.6	7.1
Period	11 (1)	338.0***	601.0***	362.6***	155.1***	31.8***
1-10 vs. 11-12	1	2639.9***	3147.5***	2155.8***	709.5***	281.6***
Diet x period	22 (2)	38.1	73.9	28.2	17.9	3.0
Collection	4 (1)	245.0***	509.6***	154.0***	63.9***	6.7
3 vs. rest	1	728.5***	-	-	-	-
Diet x collection	8 (2)	32.5	161.3	21.9	15.1	2.8
Period x collection	44 (1)	14.9	140.5	30.3	10.7	1.6
Remainder	265 (12)	12.4	49.0	22.0	7.6	1.8

[a]Test of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

**P<.05.

***P<.01.

APPENDIX C: STATISTICAL ANALYSIS OF VARIABLES IN SECTION IV

Table C1. Analysis of variance of plasma urea N and plasma cholesterol, mg/dl[a]

Source of variation	d.f.[b]		Mean squares	
			Plasma urea, N	Plasma cholesterol
Diet	2		1.8	926.6
Linear	1		3.5	1357.2**
Cecum	1		.2	352.8
diet x cecum	2		2.6	84.8
Rep (diet cecum)	6		1.0	244.9
Period	2	(1)	1.7***	154.5
Linear	1		3.3***	-
Diet x period	4	(2)	.1	113.1
Cecum x period	2	(1)	.1	102.5
Diet x cecum x period	4	(2)	.1	152.0
Remainder	12	(6)	.1	121.9

[a]Test of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

**P<.05.

***P<.01.

Table C2. Analysis of variance of apparent dry matter, cellulose and N digestibility and apparent total cellulose digestion[a]

Source of variation	d.f.[b]		Mean squares			
			Apparent digestibility, %			Apparent total cellulose digestion, g/100 kg BW daily
			Dry matter	cellulose	N	
Diet	2		392.2***	416.8	134.7***	8952.6**
Linear	1		784.0***	828.3**	268.6***	16036.7**
Cecum	1		3.7	27.4	39.5**	289.3
Diet x cecum	2		3.8	8.3	7.8	108.0
Rep (diet cecum)	6		2.7	166.4	4.5	1603.7
Period	2	(1)	89.3	940.1**	128.9***	10551.6**
Linear	1		167.8***	1878.8***	235.2***	20978.6***
Diet x period	4	(2)	4.6	51.8	15.5	1169.5
Cecum x period	2	(1)	.7	1.2	1.2	.6
Diet x cecum x period	4	(2)	1.0	7.7	1.9	67.7
Residual	12	(6)	4.4	89.4	6.8	1072.7

[a]Tests of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

**P<.05.

***P<.01.

APPENDIX D: ANALYSIS OF VARIANCE OF VARIABLES IN SECTION V

Table D1. Analysis of variance of average daily gain, plasma urea N, plasma glucose and dry matter content of cecum and colon fill

Source of variation	d.f.	Mean squares				
		Average daily gain, g	Plasma urea N, mg/dl	Plasma glucose, mg/dl	Dry matter of fill, % Cecum	Dry matter of fill, % Colon
Diet	2	4412	4.3	561.6	8.6*	44.7***
1-2 vs. 3	1	-	7.9**	1096.4*	-	-
Linear	1	-	-	-	17.2**	88.3***
Litter	7	2794	13.3***	536.1	3.5	3.4
Diet x litter	14	12137	2.1	465.5	2.3	3.4

*P<.05.

**P<.01.

***P<.10.

Table D2. Analysis of variance of empty intestinal weight, g

Source of variation	d.f.	Mean squares		
		Small intestine	Cecum	Colon
Diet	2	112411	2	83337
Litter	7	38237	511	37811
Diet x litter	13	24987	537	23461
Weight[a]	1	84631	573	141548

[a]Covariant.

Table D3. Analysis of variance of large intestine fill weight, g

Source of variation	d.f.	Mean squares			
		Dry matter		Wet	
		Cecum	Colon	Cecum	Colon
Diet	2	273	842	12310	18381
Litter	7	752	7165	28783	166763
Diet x litter	13	494	2809	17632	62896
Weight[a]	1	329	1937	21352	25823

[a]Covariant.

Table D4. Analysis of variance of cecum and colon VFA concentration, meq/100 g DM[a]

Source of variation	d.f.[b]		Mean squares					
			Cecum			Colon		
			Acetate	Propionate	Butyrate	Acetic	Propionate	Butyrate
Diet	2		81.4	90.1**	42.3**	5.9	49.4***	22.3**
Linear	1		20.4	121.3**	57.7**	1.2	96.7***	44.4***
Litter	7		83.5	66.2	7.7	31.4	14.8	9.7
Diet x litter	14		65.0	20.6	8.0	30.2	6.8	4.1
Time	2	(1)	62.4***	20.5***	11.9***	49.8***	16.1***	12.0***
Linear	1		121.5***	40.3***	23.8***	96.5***	31.5***	25.1***
Diet x time	4	(2)	1.8	.8	.2	.3	0.0	.1
Litter x time	14	(7)	1.3	.7	.2	.3	.1	.2
Remainder	27	(13)	2.3	.5	.2	.6	.2	.1

[a]Tests of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

**P<.05.

***P<.01.

Table D5. Analysis of variance of cecum and colon relative VFA concentrations, %[a]

Source of variation	d.f.[b]		Mean squares					
			Cecum			Colon		
			Acetate	Propionate	Butyrate	Acetate	Propionate	Butyrate
Diet	2		687.5**	310.3**	91.6	481.8***	169.8**	45.8
Linear	1		1014.7***	245.0**	145.4**	905.4***	242.9***	90.7**
Litter	7		306.5	176.8	28.1	93.4	42.4	44.0
Diet x litter	14		125.0	63.6	27.0	56.3	23.3	17.7
Time	2	(1)	26.5***	.7	13.8***	27.7***	1.5	9.8***
Linear	1		53.0***	.6	27.1***	53.8***	3.0**	19.4***
Diet x time	4	(2)	3.8	.9	.2	.8	.6	0.0
Litter x time	14	(7)	1.2	.7	.6	1.8	.5	.6
Residual	27	(13)	1.3	.8	.6	1.0	.5	.4

[a]Tests of significance made using conservative d.f.

[b]Conservative d.f. in parentheses.

**P<.05.

***P<.01.

Table D6. Analysis of variance of cecum and colon VFA production rates, meq/100 g DM/hr

Source of variation	d.f.	Mean squares					
		Cecum			Colon		
		Acetate	Propionate	Butyrate	Acetate	Propionate	Butyrate
Diet	2	.62	.07	.70	.22	1.35	.00
Linear	1	.09	.65	.00	.38	2.57**	.01
Litter	7	1.44	.80	.13	1.20	.49	.17
Diet x litter	14	4.01	.40	.19	1.34	.49	.19

**P<.05.